UNIVERSIDADE FEDERAL DO RIO GRANDE DO NORTE

CENTRO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

DINÂMICAS DO PICOPLÂNCTON NA COSTA OESTE DO OCEANO ATLÂNTICO EQUATORIAL

MAIARA MENEZES

ORIENTADOR: ANDRÉ MEGALI AMADO

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, da Universidade Federal do Rio Grande do Norte (PPGEco/UFRN), como parte dos requisitos necessários para obtenção do título de Mestre em ecologia, área de concentração: Ecologia Aquática.

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APRESENTAÇÃO

Esta dissertação visa compreender aspectos relacionados a área da oceanografia microbiana de baixas latitudes referente a questões ligadas especificamente à variação sazonal e aos estoques e fluxos de carbono na cadeia microbiana através da fração do picoplâncton (0.2-2µm).

Capítulo 1: DINÂMICAS DO PICOPLÂNCTON NA COSTA OESTE DO OCEANO ATLÂNTICO EQUATORIAL	
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“O conhecimento é uma ilha cercada por um oceano de mistério. Prefiro o oceano à ilha. ”

(Ludwig Wittgenstein)

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CONTENTS

ABSTRACT

Most of the ocean's biomass is microbial and picoplankton microorganisms, which consists of small cells (<3 µm), are central players of global nutrient cycle and C production. Heterotrophic bacteria, cyanobacteria (e.g. *Synechococcus* and *Prochlorococcus*) and autotrophic picoeukaryotes comprise the picoplankton and often dominate plankton in low-latitude oligotrophic oceans. Evaluate temporal dynamics of these organisms is critical to understand microbial stocks and C fluxes in the tropical ocean. Thus, we performed monthly samplings between 2013-2016 at the Equatorial Atlantic Microbial Observatory (EAMO) sampling station located on the coast of RN state – Brazil to evaluate time variations in abundance, biomass and activity (bacterial production and respiration) of picoplankton assemblage. Its relative contribution to biomass and the environmental factors that may regulate picoplankton were also investigated. Our results revealed great stability in temporal dynamic of picoplankton in a seasonal scale, despite considerable interannual variation related to El Niño (ENSO) event in 2015. Heterotrophic bacteria dominated picoplankton during the entire study period. Autotrophic picoplankton (*Synechococcus* + picoeukaryotes) contributed in average for 30% of total picoplankton biomass, and for 58% of total chlorophyll *a*. Salinity proved to be the best predictor of picoplankton, with greater abundances during periods of low salinity. However, weak environmental relationships founded may suggest a greater importance of biological interactions (as competition and/or grazing) leading to picoplankton fluctuations. This evidence provides a new perspective that picoplankton may exhibit more pronounced fluctuations in interannual intervals in the tropical region, but it is of permanent relevance for C cycling, especially in a climate change scenario.

RESUMO

A maior parte da biomassa oceânica é microbiana, e os microrganismos picoplanctônicos, que consistem de pequenas células (<3 µm), são atores centrais no ciclo global de nutrientes e da produção de C. Bactérias heterotróficas, cianobactérias (por exemplo, Synechococcus e Prochlorococcus) e picoeukaryotes autotróficos compreendem o picoplâncton e frequentemente dominam o plâncton em oceanos oligotróficos de baixa latitude. Avaliar a dinâmica temporal desses organismos é fundamental para entender os estoques e fluxos de C na região tropical. Assim, foram realizadas amostragens mensais entre 2013-2016 na estação de amostragem do Observatório Microbial do Atlântico Equatorial (EAMO) localizada no litoral do estado do RN - Brasil, para avaliar as variações temporais na abundância, biomassa e atividade (produção bacteriana e respiração) da assembleia do picoplâncton. Sua contribuição relativa à biomassa e os fatores ambientais que podem regular o picoplâncton também foram investigados. Nossos resultados revelaram grande estabilidade na dinâmica temporal do picoplâncton em uma escala sazonal, apesar da considerável variação interanual relacionada ao evento El Niño (ENSO) em 2015. As bactérias heterotróficas dominaram o picoplâncton durante todo o período do estudo, enquanto que a porção autotrófica (*Synechococcus* + picoeukaryotes) contribuiu em média com 30% da biomassa total de picoplâncton e com 58% do total de clorofila *a*. A salinidade se mostrou como o melhor preditor do picoplâncton, com maiores abundâncias ocorrendo em períodos de queda na salinidade. No entanto, as fracas relações ambientais encontradas podem sugerir maior importância de interações biológicas (como competição e / ou pastoreio) levando a flutuações do picoplâncton. Essas evidências fornecem uma nova perspectiva de que o picoplâncton pode exibir flutuações mais acentuadas em intervalos interanuais na região tropical, porém é permanente sua relevância para a ciclagem do C, principalmente em um cenário de mudanças climáticas.

INTRODUCTION

The ocean is the largest ecosystem in the world and plays an important role in nutrient's stocks and flows in our biosphere (Falkowski *et al.*, 1998; Arrigo, 2005). Global nutrient cycling in oceans is mainly driven by marine microbes known as plankton, which lead organic C production in pelagic waters and forms the base of the marine food web (Fenchel, 1988, Sherr & Sherr, 1988; Azam & Worden, 2004). The smallest size-class of plankton (cells < 3 µm, Sieburth *et al.*, 1978; Vaulot *et al.*, 2008), or picoplankton, is composed by heterotrophic bacteria and autotrophic phytoplankton (cyanobacteria and picoeukaryotes). These worldwide-distributed cells dominate microbial standing stocks in most part of oceans. Prokaryotes reach up 10^9 cells L^{-1}, jointly with virus (Kirchman, 2008). Picoeukaryotes although less abundant than prokaryotes, often contribute to a significant portion (60-80%) of microbial biomass, due to being slightly larger (Not *et al.*, 2009; Marie *et al.*, 2010, Massana, 2011).

Since the 70's, science has made efforts to understand the relative importance of picoplankton for C stocks and fluxes in aquatic ecosystems (e.g. Pomeroy, 1974; Waterbury, 1979). A general trend is that the relative importance of smaller organisms (e.g. picoplankton) increases with increasing oligotrophy (Gasol & Duarte, 2000). Low nutrient supply ensure competitive advantage to picoplankton due higher surface:volume ratios also by ability to use resources more efficiently than larger cells (Taylor *et al.*, 2015; Lewis, 1986; Agawin & Agustí, 2005). As the tropical ocean is usually oligotrophic, microbial food web and microbial loop (process in which C in bacterial compartment return to higher trophic levels via its predation by microzooplankton, see Azam *et al.*, 1983) may set main trophic pathways. The fact that smaller body size structure have greater relative contribution in the tropics has been well accepted for marine (Herbland *et al.*, 1985; Marañon *et al.*, 2000; Pérez *et al.*, 2005) and freshwater environments (Sarmento, 2012).While in colder and nutrient rich waters of higher latitudes classical food chain dominates, maintained by larger organisms (Legendre & Rassoulzadegan, 1995).

Latitudinal gradients influence nutrients (e.g. N and P) availability and stoichiometry in the ocean, which, in turn, may affect picoplankton metabolism (Martiny *et al.*, 2013). For example, bacteria uses algal-derived carbon more efficiently for biomass production in more eutrophic systems, as polar and temperate regions (Gasol & Duarte, 2000). In contrast, in oligotrophic tropical waters high respiration rates reduces bacterial growth efficiency - BGE (White *et al.*, 1991; del Giorgio & Duarte, 2002; Amado *et al.*,

2013). The nutrient depletion in superficial waters of low latitudes possibly reflects the difference in light intensity affecting the sestonic C:nutrient ratio (Sterner *et al.*, 1998) as well stratification processes. Solar radiation and attenuation of light in water column is another key factor influencing picoplankton composition, distribution, and dominance patterns across spatial scales, from latitudes (Schattenhofer *et al.*, 2009), coastal versus open-ocean waters (Partensky *et al.*, 1996), and in vertical profiles in water column (Moore *et al.*, 1995). Considering the relatively time-stable high temperatures and the nutrient depletion in most tropical regions (except from rivers discharges and upwelling areas), is not surprising that bacteria commonly dominates microbial abundance and C production near equator (Fuhrman *et al.*, 1989; Hoppe *et al.*, 2002, Bergo *et al.*, 2017).

Equatorial oceans have predominant time stable environmental conditions that ensure picoplankton dominance year around. In equatorial Pacific, there are minor seasonal influences but clear inter-annual patterns in picoplankton, mainly influenced by El Niño South Oscillation/ENSO (Dandonneau *et al.*, 2004), with significant reduction of larger phytoplankton groups (Bidigare & Ondrusek, 1996). In equatorial Atlantic, despite seasonal variations (Xie *et al.*, 2004), currents (North Brazil Current) carry warm and nutrient-poor waters to the north and northeast Brazilian coast, making persistent the oligotrophy condition (Longhrust & Pauly, 1987). However, most studies in this area were Lagrangian sampling strategies (Zubkov *et al.*, 1998; Marañon *et al.*, 2000; Hoppe *et al.*, 2002; Moreno-Ostos *et al.*, 2011), while time-series studies of microbial observatories (Eulerian sampling) were carried out in temperate (WCO-Western English Channel; BBMO-Blanes Bay) or subtropical regions (SPOT-San Pedro California; BATS-Sargasso Sea) of the northern hemisphere. Still, studies of picoplankton along the Brazilian coast were only carried out on the South-Southeast region (Andrade *et al.*, 2004; Moser *et al.*, 2016; Bergo *et al.*, 2017), which contrast by seasonal dynamic with oceanic intrusions and high productivity events.

Here we provide the first study that evaluate the temporal dynamic of picoplankton in the Western equatorial Atlantic – NE Brazilian coast. Our goal was to address and discuss the following questions: (1) Can seasonality explain the dynamic of picoplankton in this scenario of greater environmental stability? (2) What is the contribution of the picoplankton size fraction to the C budget, considering autotrophic and heterotrophic organisms? (3) Which environmental factors regulates picoplankton abundance and metabolism (of heterotrophic fraction) in this coastal region of western Atlantic? We hypothesized that seasonality has a weak influence on the picoplankton in

western equatorial Atlantic, since the seasonal signal is low compared to more dynamic and predictable coastal areas of higher latitude oceans. In addition, picophytoplankton will contribute significantly to the total phytoplankton biomass even considering the coastal environment; even that we expect the prevalence of heterotrophic bacteria.

METHODS

Study site and environmental measures

We performed monthly samplings from February 2013 to August 2016 in the Equatorial Atlantic Microbial Observatory - EAMO, located in Rio Grande do Norte State, Northeast Brazil - S 05º 59' 20,7"/W 035º 05' 14,6", 3 km from the coastline (Fig. 1). The sampling station is located within the narrow continental shelf (15-30km, Fig.S1), more specifically at the interface between the internal and external shelves, with depths up to 20 m depth, where longshore currents flow from south to north (Vital *et al.*, 2010). High atmospheric temperatures (26-28°C) prevail along the year and seasonality is marked by rainfall. Historically short rainy period of approximately 3 months occurs between April and June, while a longer dry period occurs between September and December (Nimer, 1989). The displacement of the Inter-Tropical Convergence Zone (ITCZ) and trade wind forces are principal causes of seasonal variations (Silva *et al.*, 2009; Castellanos *et al.*, 2015). In the intention to classify rainy (March to July) and dry (August to February) seasons, we used the historical climatic data of the last 50 years (data from National Institute of Meteorology - Instituto Nacional de Meteorologia - INMET; Fig. S2).

We carried out vertical profiles of temperature and salinity using a multiparameter probe (Horiba U-50 Series). We estimated the euphotic zone by associating Secchi disk measurements (*Zeu*, depth at which light is 1% of subsurface light) and the vertical light attenuation coefficient for coastal waters (*sensu* Luhtala & Tolvanen 2013; see Table S1 for conversion coefficients). We collected seawater samples (20 L) in subsurface (~1m depth) and immediately passed through a 120µm mesh to remove large planktonic organisms. Samples were then stored in a dark bottle and brought to the laboratory for further analysis (maximum 2 hours after sampling).

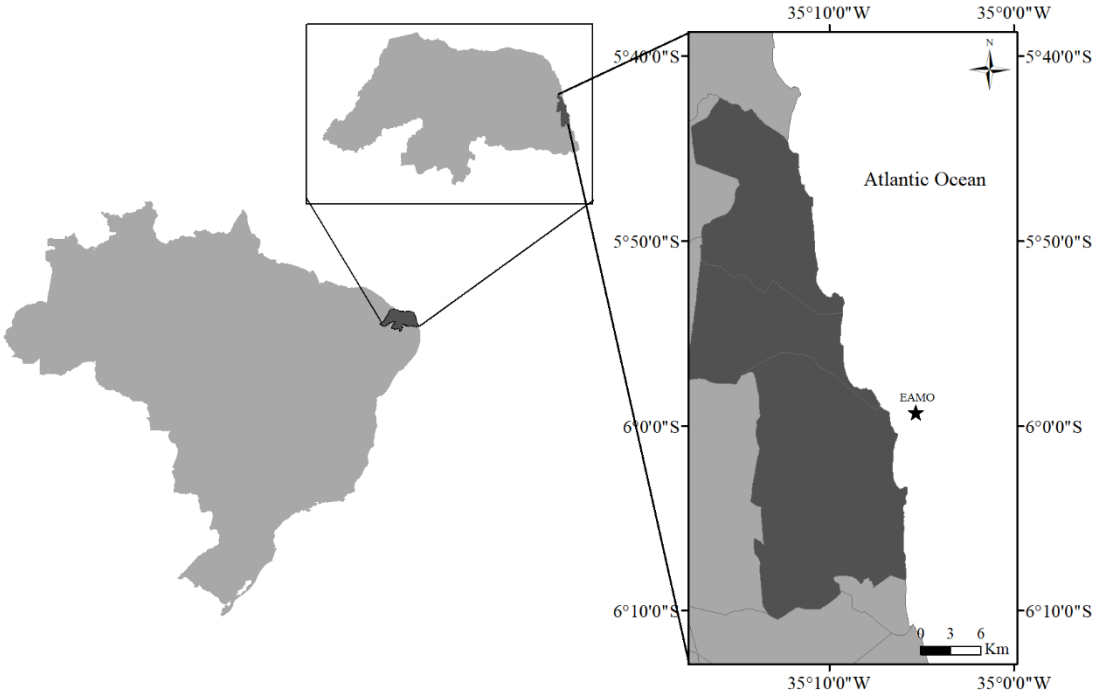

Figure 1: Map of the Northeast Brazil coast showing the location of the Equatorial Atlantic Microbial Observatory.

Total chlorophyll *a* concentration was obtained by filtering ~2 L seawater on Macherey-Nagel GF-5 glass microfiber filters (average particles retention of 0.45 μm). Seawater samples were also filtered through polycarbonate membranes of 3μm Millipore® to estimate picoplankton chl *a* fraction (< 3 μm). Filters were kept frozen at -80°C until extraction with 90% acetone. GF-5 filtered water was used to estimate concentration of dissolved nutrients (N and P), stored in 50 ml falcons and frozen until analysis at -80°C.

We collected cumulative monthly rainfall data from the National Institute of Meteorology (INMET) database. Additional environmental data of chlorophyll *a* concentration, downwelling attenuation coefficient at 490 nm (K490 - a proxy of turbidity), were collected in the Plymouth Marine Institute database, provided by Centro de Previsão de Tempo e Estudos Climáticos-CPTEC/INPE. As the same for photosynthetically available radiation (PAR) and concentration of particulate organic carbon (POC), obtained in the MODIS aqua database. South Oscillation Index data collected online available in:

https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/

Analytical procedures

We estimated chlorophyll *a* concentration as in Welschmeyer (1994) through reading fluorescence in TD-700 fluorimeter (Moreno-Ostos, 2012). For dissolved nutrients, all analyses followed conventional methods (Grasshoff *et al.*, 1999), conducted by an Auto Analyser 3 (AA3 HR Seal). Ammonium measurements were performed by the blue indophenol method (Parsons *et al.*, 1984) with detection limits of 0.1 We determined Nitrite concentration by the diazotization method. Nitrate and Total N were determined by reduction in Cd-Cu column followed by diazotization, analyzed by Flow Injection Analysis System (FIAS). Dissolved organic N was estimated based on the difference between Total N and the sum of dissolved inorganic N forms: Ammonium, Nitrite and Nitrate. Soluble Reactive P and Total P concentrations were determined through phosphomolybdic method. Total fractions of P and N were digested in acid medium with potassium persulfate before analyses. Inferences about nutrient limitation (N and P) were performed through ratio between Nitrate + Nitrite and soluble reactive P, for new production and Total N : Total P ratio was used to compare with Redfield ratio (N:P as 16:1; Redfield *et al.*, 1963). Determination of dissolved inorganic silicate was based on the formation of a yellow silicomolybdic acid.

For picoplankton abundance, samples (1.6 mL) were preserved with 1% paraformaldehyde + 0.05% glutaraldehyde (final conc.) and frozen at -80°C (Marie *et al.*, 1996). Cell abundance was determined by flow cytometry (BD FACScalibur) equipped with a blue laser (emission at 488 nm) (Marie *et al.*, 1996). For Heterotrophic bacteria (HB) 300 µl were stained with 3 µl SYBRGreen (Molecular probes) (Marie *et al.*, 1997), let 10 min in the dark before running at Low speed (ca. 9.18 µl min^{-1}). HB cells were detected by their signature in a plot of SSC (90° side scatter) *vs.* FL1 (green fluorescence), and in FL3 (red fluorescence) *vs.* FL1 as showed in Fig.2 A and B, according to del Giorgio *et al.*, (1996) and Gasol and del Giorgio (2000). For *Synechococcus* and autotrophic picoeukaryotes, 400 µl non-stained samples were run at Hi speed (ca. 52.3 µl min^{-1}). Figure 2C and D shows cytograms of SSC *vs.* FL3, and FL3 *vs.* FL2 (orange fluorescence) used to detect autotrophic cells. Data were acquired in log mode until around 10000 events or during 3 min. 1µm Polysciences latex beads (10µl) were used for calibration proposes. Data acquisition and analysis were performed with the software FlowJo® V10.0.8.

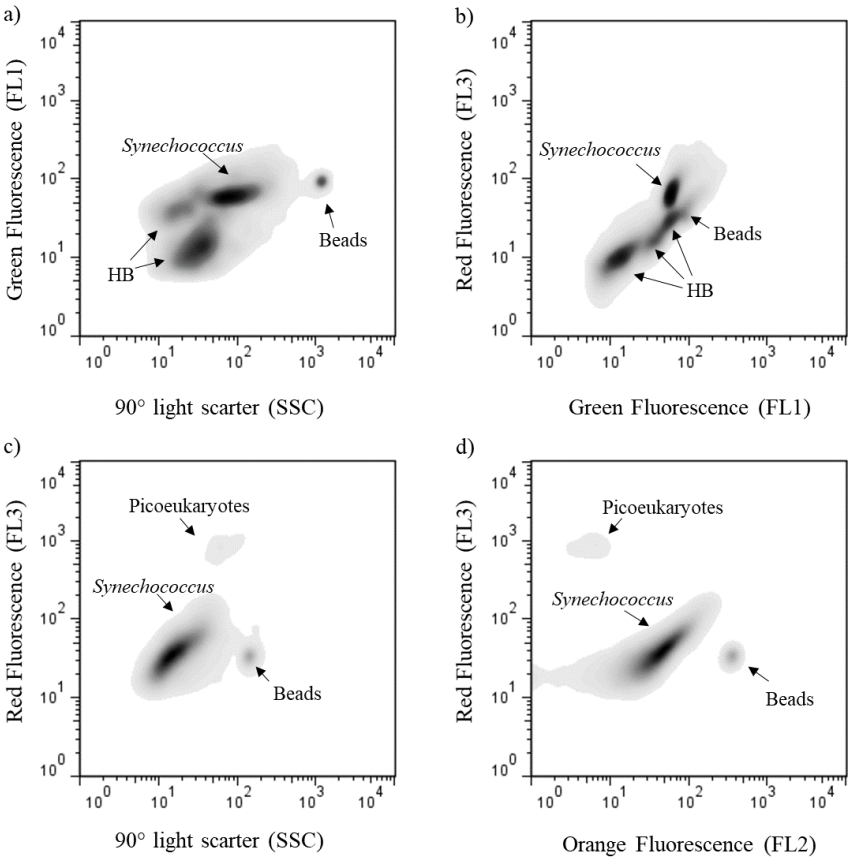

Figure 2: Density plots obtained by flow cytometry Equatorial Atlantic Microbial Observatory (EAMO) water samples. (A and B) The Syto-13 stained picoplankton samples. Identification of the three populations of Heterotrophic Bacteria (HB), Synechococcus spp. and the polysciences 1 mm beads. (C and D) Unstained samples showing the red and orange autofluorescence of autotrophic picoplankton groups: Synechococcus spp. and picoeukaryotes.

HB biovolume was estimated using DNA related fluorescence (FL1) as a surrogate of bacterial size average relative to beads (Gasol and del Giorgio, 2000). Then, bacterial biomass was calculated using the volume-to-carbon relationship where fg C cell^{-1} = 120 fg (µm³ cell^{-1})$^{0.7}$ (Norland & Tumyr, 1987). Picocyanobacteria and autotrophic picoeukaryotes biomass was calculated assuming spherically shaped cells and cell carbon conversion factors of 82 fg C cell^{-1} for *Synechococcus* and 530 fg C cell^{-1} for Picoeukaryotes (Worden, 2004).

Bacterial production (BP) rates were estimated using the [^{3}H]-leucine incorporation method (Kirchman, 1992). Briefly, 15 µl of [^{3}H]-leucine (20 nM final conc.) were added to six 1.2 ml replicates (4 treatments and 2 dead controls) After incubation period (~2:30h) in dark in situ temperature, leucine incorporation was stopped

by adding 90 µl of 100% trichloroacetic acid (TCA) and samples were stored frozen (-80ºC) until further analyses. We extracted bacterial protein by a washing with 5% TCA and 80% ethanol (Smith and Azam, 1992) and read in a liquid scintillation counter (Beckman LS – 6500). Disintegrations were converted to µg C l^{-1} h^{-1} using the conversion factor of 0.86 from Smith and Azam (1992).

Bacterial respiration (BR) rates were estimated by dissolved oxygen consumption in 5.9 mL exetainers® (10 replicates) on 48 h incubation period at dark in situ temperature. Initial and final dissolved oxygen concentrations were measured using a micro-probe connected to OXY-meter Unisense© (Briand *et al.*, 2004). Estimations were performed assuming a respiratory quotient (RQ) of 1 (see Berggren *et al.*, 2011).

Statistical analysis

For statistical analyses, we filled gaps in the chlorophyll *a* data, that were lost during analysis procedures (N=19/43), with alternative data obtained through satellite imagery (MODIS aqua, see the methods). The slope found for the relationship between the data collected in the field and satellite data was 0.77 (R^2 = 0.19; p = 0.06). Therefore, estimated values of chl *a* followed equation: Chl *a* = 0.77(Chl *a* satellite) + 0.09.

To investigate potential violations on the independence assumption, we performed a temporal correlation analysis comparing simple linear models of the dependent variables with residual auto-correlation structure and auto-regressive model of order 1 (Zuur *et al.*, 2009). Only HB showed auto-correlation structure. However, because of low correlation index (rho = 4.90 x 10^{-8}) we assumed absence of autocorrelation on data. Furthermore, there was no model improvement with both the auto-correlation (AIC = 24.5, BIC = 31.5) and the autoregressive models (AIC = 24.5, BIC = 31.5) compared with simple linear model (AIC 22.5, BIC = 28.1).

We performed comparative t-tests of each environmental and biological (picoplankton) variable between seasons. We tested homoscedasticity with Barlett test, and for heteroscedastic variables, we used Welch t-tests. Multicolinearity between variables was detected through Variance Inflation Factor (VIF), assuming a VIF=10 for exclude collinear variables. Pearson correlation analyses were performed between all environmental parameters and picoplankton components, as well as between them. Additional regression analyses (model I) were performed. All analyses were performed in R 3.4.1 (R Development Core Team).

RESULTS

Environmental seasonality and water column structure

Rainfall revealed seasonal and interannual variation over the study period. During rainy seasons (March-July), the average rainfall was more than three times greater than dry seasons (August-February, see Tab.1), with maximum values recorded in June-July periods, and minimum in October-December. We observed a gradual reduction on average of cumulative rainfall of dry and rainy seasons throughout the study period (Tab. 1). Cumulative rainfall for both seasons in 2016 were below that from previous years and there was a 74% reduction in total annual average of rainfall from 2016 relative to 2013.

Table 1: Seasonal and annual averages (±SD) and total cumulative rainfall (mm) along 2013-2016 in NE coast of RN-Brazil, data from INMET.

	Dry season	Rainy season	Annual
2013	90.1 ± 93.1 632.9	259.1 ± 162.9 1295.3	168.8 ± 152.3 1856.9
2014	60.9 ± 47.2 426.1	261.4 ±170.2 1306.8	146.3 ± 148.3 1756.0
2015	58.9 ± 47.3 412.0	232.1 ± 113.2 1160.4	121.1 ± 120.7 1452.7
2016	53.9 ± 23.8 377.6	114.3 ± 63.1 721.7	44.7 ± 20.8 1178.8

Sea surface temperature did not varied according to rainfall seasonality, but followed closely atmospheric temperature (Fig. 3). Higher temperatures occurred during austral summer (January-March), ranging from 25.9 to 29.6 °C and usually peaked in April. Whereas lower temperatures (< 27,5°C) occurred from June to September, with minimal in July-August period. PAR was on average higher during dry seasons (36.07 - 56.78 Einstein m^{-2} $day^{-}1$; Tab.2), while POC concentrations were higher during rainy season (86.36 - 400.2 mg m^{-3}). Euphotic zone depth (range 6.64 - 25.65 m) did not differed between rainy and dry seasons, as well as K490 (range 0.06 to 0.18), TDS (range 31.2 - 37.6) and salinity (range 3.27- 3.79). Water column was vertically stable in terms of temperature, but slightly warmer during dry seasons (1.5°C; Fig. S4 *a* and *b*); when dissolved oxygen showed higher concentrations. Dissolved oxygen maximum concentrations were recorded near 2m in both seasons (Fig. S4 *c* and *d*).

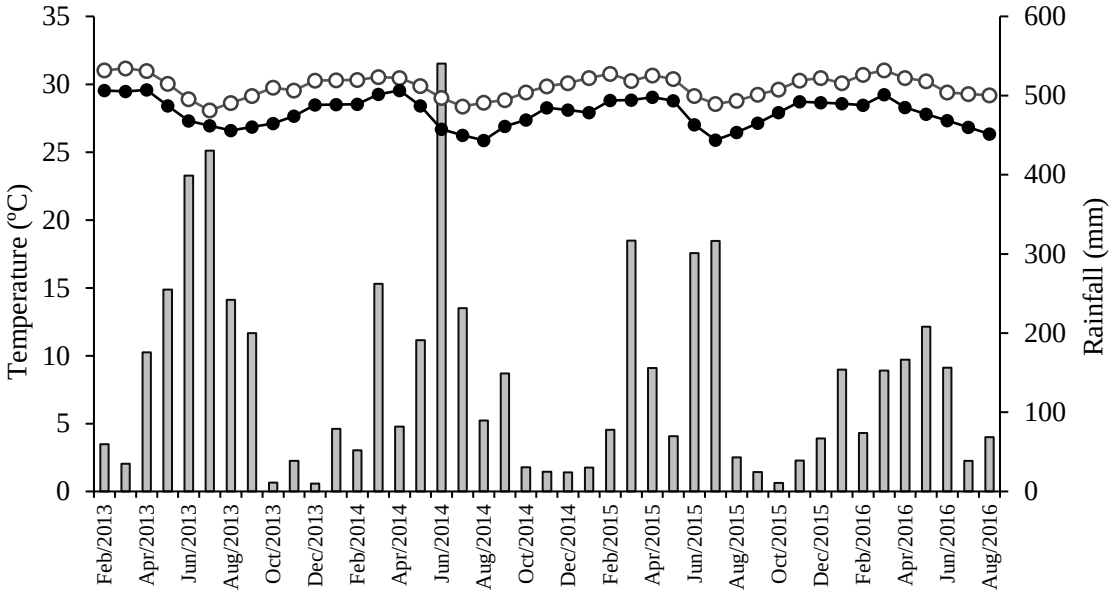

Figure 3: Sea-surface (filled circles) and atmospheric (open circles) temperatures, and monthly-accumulated rainfall seasonality in the Northeast Brazilian coast between 2013 and 2016.

Table 2: Comparative descriptive statistics (mean, standard deviation and coefficient of variation) of environmental variables and picoplankton abundance between dry and rainy seasons in western equatorial Atlantic coast. (SST = Sea Surface Temperature, Zeu = Euphotic zone, K490 = Downwelling Attenuation Coefficient at 490nm.T-statistics, of Welch t-test comparing seasons with degree of freedom and significance (p-value in bold) are given.

		Dry seasons	Rainy seasons	t-value	df	p-value
Rainfall	(mm)	68.33 (± 83.43)	224.21 (± 132.85)	-4.81	26.2	**<0.001**
SST	(ºC)	27.73 (± 0.66)	28.19 (± 1.21)	-1.18	32.0	0.243
PAR	(Einstein m^{-2} day^{-1})	51.78 (± 3.38)	42.98 (± 5.92)	7.69	31.2	**<0.001**
POC	(mg m^{-3})	128.63 (± 20.01)	184.82 (± 87.97)	-2.51	27.5	**0.018**
Zeu	(m)	10.87 (± 5.40)	13.09 (± 2.43)	-1.43	32.0	0.161
K490	r.u.	0.089 (± 0.02)	0.091 (± 0.03)	-0.16	41.0	0.874
TDS	(g L^{-1})	33.94 (± 1.84)	33.82 (± 1.84)	0.19	32.0	0.847
Salinity	r.u.	3.53 (± 0.16)	3.54 (± 0.08)	-0.16	32.0	0.868
NH^{4+}	(µM)	1.83 (± 1.09)	1.65 (± 1.00)	0.96	18.8	0.35
NO^{2-}	(µM)	0.05 (± 0.09)	0.08 (± 0.09)	-2.31	18.7	**0.03**
NO^{3-}	(µM)	1.19 (± 1.77)	1.24 (± 1.64)	-0.63	16.9	0.54
NT	(µM)	9.64 (±4.79)	8.40 (± 3.39)	0.80	13.9	0.44
PO_4^{3-}	(µM)	0.06 (±0.02)	0.06 (± 0.02)	0.23	17.3	0.82
PT	(µM)	0.30 (±0.11)	0.30 (± 0.09)	-0.59	14.1	0.56
SiO_2	(µM)	2.72 (± 2.01)	3.363 (± 2.68)	0.24	24.0	0.81

Total N concentrations was on average 8.93 µM (ranged from 2.67 up to 20 µM) and did not present any clear seasonal pattern as the others dissolved N and P forms but revealed a tendency to decrease to the end of the study (see Fig. S4). Ammonium was 0.72 µM on average (ranged from 0.21 to 4.97 µM), while nitrate concentrations were 1.22 µM on average (ranged from 0.05 to 5.87 µM) and peaks were usually recorded in June-July (Fig.S4*c*). Nitrite were on average 0.07 µM (ranged <0.01 to 0.34 µM) and was the only nutrient that differed between seasons with higher concentrations during rainy seasons (Tab.2). Most of the N in the water was in the organic form, averaging 66% (± 1.79; reaching up 95% of TN). Soluble reactive P average was 0.06 µM (range 0.12 - 0.03 µM), while Total P average was 0.3 µM (range 0.46 - 0.1 µM, see Fig. S5 for more details). The ratio Nitrate + Nitrite : Soluble Reactive P was an average 19.2: 1, but showed great variation between 80: 1 to 1: 1, while the average of Total N : Total P ratio was 33:1, ranging from 79.6:1 to 8.5:1.

Temporal dynamic of picoplankton

Heterotrophic bacteria dominated picoplankton abundance during all study period of 8.01 x 10^5 cells ml^{-1} on average (range 1.4 - 19.5 x10^5 cells ml^{-1}), while *Synechococcus* spp. was one order of magnitude lower, with 8.7 x 10^4 cells ml^{-1} on average (range 3.9 – 17.8 x 10^4 cells ml^{-1}). Picoeukaryotes presented the lowest abundance of the study, with 1.6 x 10^3 cells ml^{-1} on average (0.4 – 4.9 x 10^3 cells ml^{-1}). Heterotrophic bacteria and picoeukaryotes usually peaked in July months (Fig. 4*a* and *c*), although their abundances did not differ between seasons (Tab.3). In contrast, *Synechococcus* showed higher abundances during dry seasons (Fig. 6*b*). *Synechococcus* (slope = 0.27, R^2 = 0.11, p-value**:** 0.063) and picoeukaryotes (slope = 0.47, R^2 = 0.12, p-value: 0.058) showed marginally significant positive relations with HB. However, we found no significant relationship between the two autotrophic picoplankton populations.

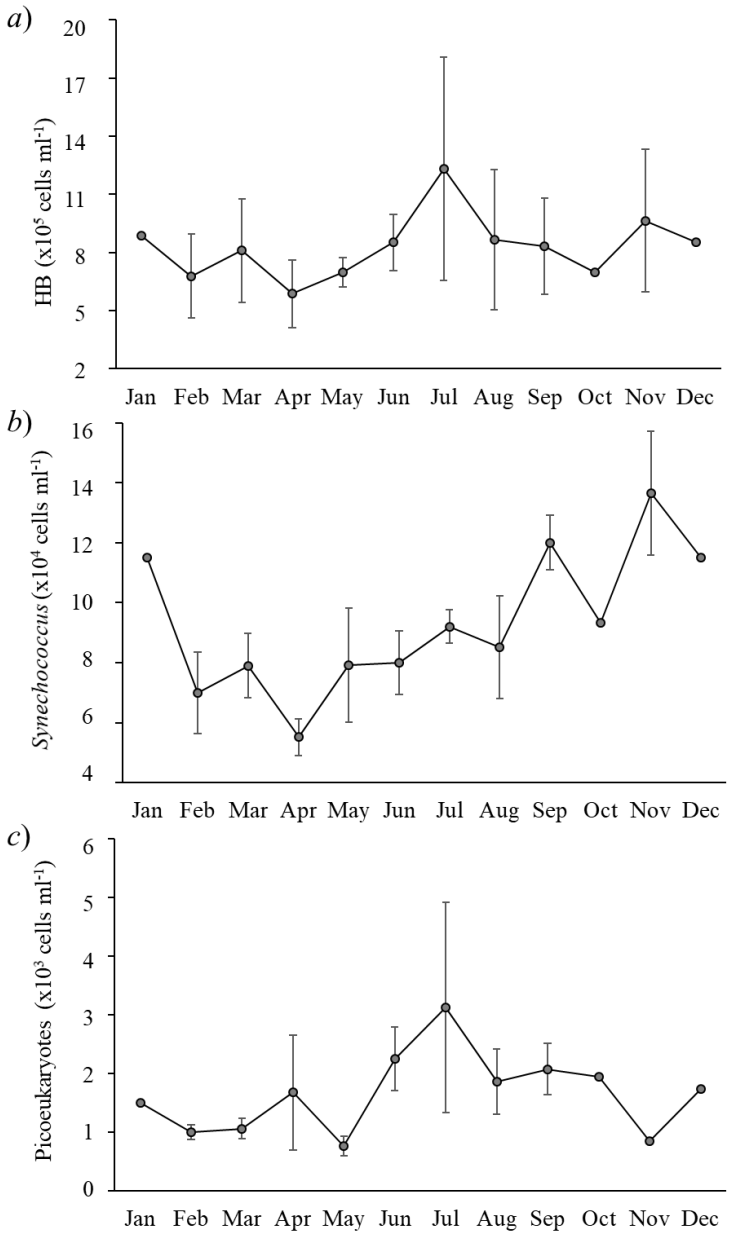

Figure 4: Seasonal variation of cells abundance of *a)* Heterotrophic Bacteria, *b) Synechococcus* spp. and *c)* Picoeukaryotes (average ±SE per month) in western equatorial Atlantic coast during 2013-2016). Note different scales between graph.

Table 3: Comparative descriptive statistics of chl*a*, picoplankton abundance, biomass and metabolic rates between dry and rainy seasons (mean ± sd) in western equatorial Atlantic coast. T-statistics of Welch t-test, degrees of freedom and significance ($p \leq 0.05$) are given.

		Dry season	Rainy season	t-value	df	p-value
Total chl-*a*	(µg L^{-1})	0.39 (± 0.20)	0.68 (± 0.31)	0.08	41	0.94
> 3µm chl-*a*	(µg L^{-1})	0.28 (± 0.21)	0.23 (± 0.13)	0.69	21	0.50
< 3µm chl-*a*	(µg L^{-1})	0.40 (± 0.27)	0.30 (± 0.16)	0.98	21	0.34
HB	(10^5 cells ml^{-1})	8.23 (± 4.65)	7.97 (± 4.17)	0.08	31	0.93
Syn	(10^4 cells ml^{-1})	9.96 (± 3.49)	7.53 (± 2.23)	2.09	31	**0.04**
Peuk	(10^3 cells ml^{-1})	1.50 (± 0.73)	1.67 (± 1.40)	-0.56	31	0.58
HB biomass	(µg C L^{-1})	18.83 (± 10.50)	18.14 (± 9.73)	0.14	31	0.88
Syn biomass	(µg C L^{-1})	8.17 (± 2.86)	6.17 (± 1.83)	1.65	22	0.11
Peuk biomass	(µg C L^{-1})	0.77 (± 0.39)	0.89 (± 0.74)	-0.78	26	0.44
BP	(µg C L^{-1} h^{-1})	1.66 (± 2.27)	1.49 (±0.95)	0.29	29	0.77
BR	(µg C L^{-1} h^{-1})	9.37 (± 8.62)	12.07 (± 9.34)	-0.75	23	0.46

Inter-annual variation revealed peaks in abundance of all picoplankton components coinciding with period of significant rainfall reduction in 2015-2016. Anomalous rainfall reduction at this period was related to more negative Southern Oscillation Index (SOI) values (Fig. 5), which denotes El Niño episodes in the tropical Pacific. Regression analysis revealed a significant negative relation between SOI and picoeukaryotes abundance ($r^2 = 0.16$, $p = 0.02$, Fig. 10*a*), which did not occur with the prokaryotes components (HB and *Synechococcus*). However, grouping all prokaryotes and eukaryotes into a single variable (Total picoplankton - TPP), we assessed the same negative relation ($r^2 = 0.20$, $p = 0.01$, Fig 10*b*).

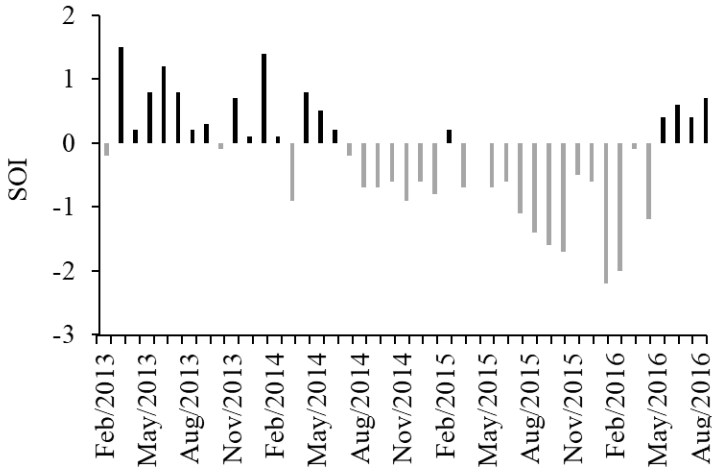

Figure 5: South Oscillation Index (SOI) measured between 2013-2016. Data from: NOAA.

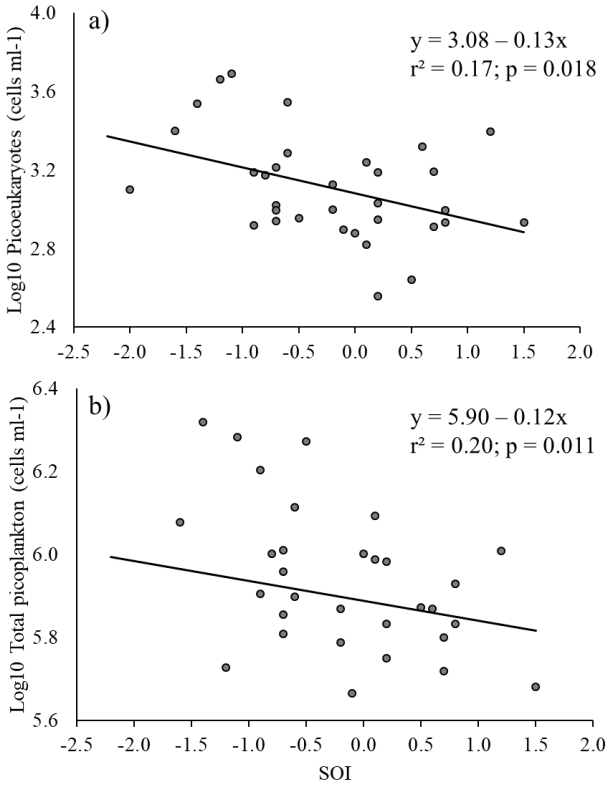

Figure 6: Regression analysis of Southern Oscillation Index (SOI) with *a*) picoeukaryotes and *b*) total picoplankton abundances in western equatorial Atlantic coast (2013-2016.)

Picoplankton chl *a* (chlorophyll in the < 3µm size fraction) did not present significant seasonal variation along the study, following the same patterns of total chl *a* and the nano-microphytoplankton chl *a* (> 3 µm size fraction, Tab. 3). Total chl *a* was 0.56 µg l^{-1} on average (ranged from 0.17 to 1.61 µg l^{-1}). Picoplankton chl *a* average was 0.27 µg m^{-3} (0.12 - 0.95 µg m^{-3}), while average of nano-microphytoplankton was 0.25 µg.m^{-3} (0.05 - 0.66 µg.m^{-3}). Relative contribution of picoplankton for total chl*a* ranged from 14 to 82%, with average of 58% (Fig. 7). However, chl *a* of pico- and nano-microphytoplankton did not differ significantly from each other (t = -1.66, df = 41.02, p = 0.105) contributing in a similar way for total chl *a*. The highest contributions of pico- to total chl*a* occurred between December to February, when total chl*a* was relatively low, while the minimum contribution occurred during August.

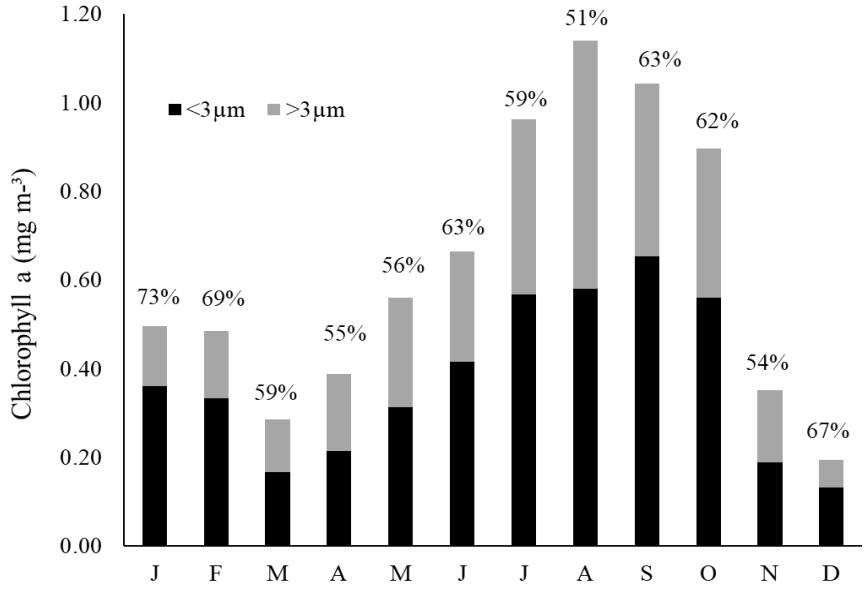

Figure 7: Monthly average contribution (%) of photoautotrophic picoplankton (<3µm-black bars) and micro-nanoplankton (>3µm - gray bars) to total chl-*a* concentration at the western equatorial Atlantic along 2013-2016.

HB biomass was 18.8 µg C L^{-1} on average (range 2.97 - 44.10), while *Synechococccus* and picoeukaryotes were 7.54 µg C L^{-1} (range 3.16–14.60) and 0.86 µg C L^{-1} (range 0.19 – 2.60), respectively. There was no seasonal variation in the biomass for any picoplankton component (Tab.3). Relative contribution of *Synechococcus spp.* was 27.6% on average (range 20-34%), and picoeukaryotes contributed only with on average 3.2% (range 1-5%) to total picoplankton biomass. Maximum contribution of HB to total picoplankton biomass (75%) occurred in July and August (Fig.8), when the contribution of *Synechococcus* spp. for biomass was lower (20-21%). For picoeukaryotes, maximum contribution (5%) occurred in April months and remained slightly higher until October months.

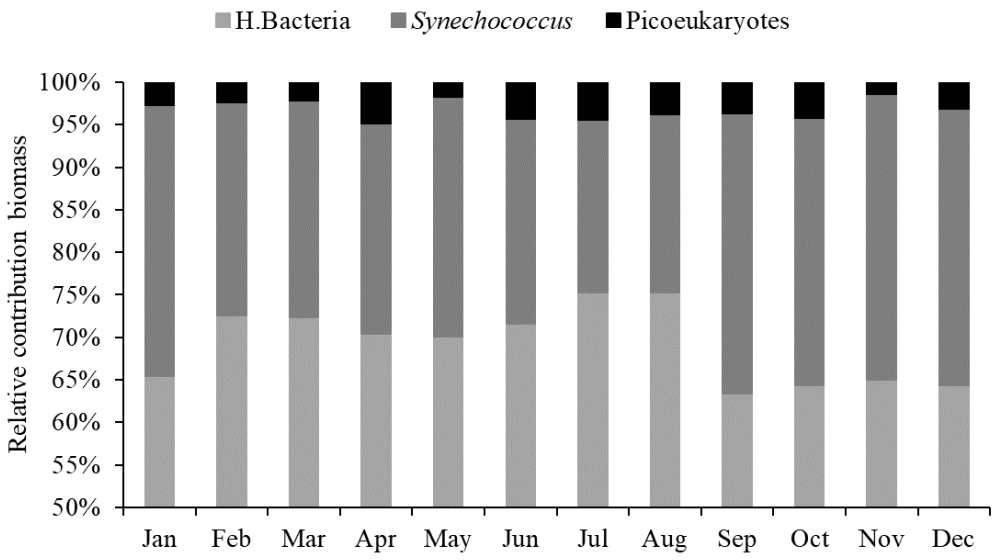

Figure 8: Mean relative contribution of Heterotrophic bacteria, *Synechococcus* and Picoeukaryotes for C biomass (µg C L^{-1}) per month, from February 2013 to August 2016, western equatorial Atlantic coast. Note that y-axes begins in 50%.

Bacterial Production and Respiration

Bacterial production (BP) ranged from 0.15 to 8.76 µg C l^{-1} h^{-1}, and showed no seasonal variation during the study period (see Tab.3). Overall, all months recorded BP mean values below 4 µg C l^{-1} h^{-1}, with exception of September 2015 (Fig. 9*a*). Bacterial Respiration (BR) ranged from 2.01 to 35.07 µg C l^{-1} h^{-1} and did not show seasonal variation as BP. Rates and variability of BR (among replicates) was much higher in 2013, until September 2014 (Fig. 9*b*). After this period, the recorded rates (<12.5 µg C l^{-1} h^{-1}) and variability were lower. Despite all this irregular variance, it was possible to observe that there were regular annual peaks occurring between March and April in BR (Fig. 9*b*). Bacterial growth efficiency (BGE) was 17% on average (ranged from 1 to 48%), while bacterial carbon demand (BCD) was on average 11.51 µg C l^{-1} h^{-1} (ranged from 2.34 to 35.83 µg C l^{-1} h^{-1}).

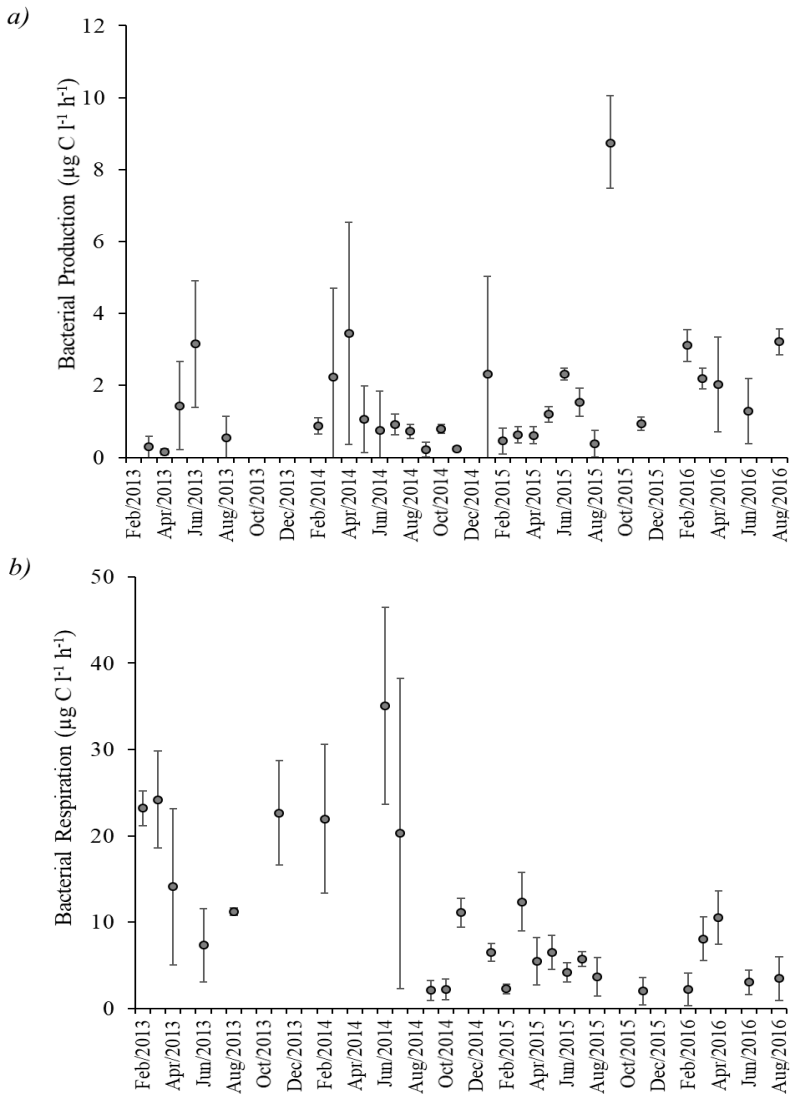

Figure 9: Average and standard deviation of a) bacterial production and b) respiration in the western equatorial Atlantic coast along 2013-2016 period.

Environmental drivers of picoplankton

None of the environmental variables, including the nutrients concentrations, correlated significantly with HB, except for salinity (Tab.4). There were negative relations between salinity and *Synechococcus* spp., picoeukaryotes, and with TPP. S*ynechococcus* revealed a negative significant correlation with rainfall, and was positively correlated to PAR, ammonia and TN. Picoeukaryotes were negatively correlated with SST, and positively correlated with POC, nitrite and silicate. Total chl*a* correlated negatively with SST, *Zeu* and salinity, and positively with POC, TDS and silicate. BP correlated negatively only with ammonia, while BR correlated negatively

with TDS, nitrite and silicate. None of the picoplankton variables reported correlations with K490, soluble reactive phosphorus or total phosphorus.

Table 4: Pearson's correlations between picoplankton and environmental variables. In bold, significant relationships are given as : * ≤0.05; ** ≤0.01;*** ≤0.001.

	HB	Syn	Peuk	TPP	Total Chl*a*	BP	BR
Rainfall	-0.09	**-0.46****	0.08	-0.16	0.25	0.05	0.17
SST	-0.22	-0.20	**-0.53*****	-0.22	**-0.63*****	-0.09	0.15
PAR	0.02	**0.37***	0.12	0.15	-0.01	-0.19	-0.05
POC	0.31	0.12	**0.62*****	0.31	**0.41****	0.07	0.01
Zeu	-0.03	0.00	-0.29	-0.09	**-0.58*****	0.09	0.11
k490	0.25	0.24	0.17	0.21	0.27	-0.16	0.25
TDS	-0.16	-0.32	0.24	-0.03	**0.34***	0.20	**-0.45***
Sal	**-0.50*****	**-0.44****	**-0.35***	**-0.41***	**-0.42****	-0.13	0.13
NH^{4+}	0.06	**0.44***	0.13	0.05	0.01	**-0.45***	-0.05
NO^{2-}	-0.07	-0.12	**0.53****	0.29	0.29	0.30	**-0.44***
NO^{3-}	-0.06	0.19	0.29	0.09	-0.05	0.12	-0.20
TN	0.16	**0.57***	0.32	0.14	-0.21	-0.25	0.08
PO_4^{3-}	-0.04	0.15	0.25	0.01	0.01	-0.05	0.06
TP	-0.23	0.11	0.22	-0.17	-0.14	0.19	-0.34
SiO_2	0.05	0.01	**0.63*****	0.32	**0.41***	0.34	**-0.61****

Table 5: Pearson's correlation matrix between picoplankton components, metabolic rates and chla. Correlation coefficients are above principal diagonal, while p-values (0.05 of significance) are below.

	HB	Syn	Peuk	TPP	Total Chl*a*	BP	BR
HB	1	**0.56**	**0.41**	**1.00**	0.28	0.17	-0.19
Syn	**0.001**	1	0.28	0.54	0.01	-0.08	-0.11
Peuk	**0.016**	0.109	1	**0.48**	**0.57**	**0.41**	-0.36
TPP	**0.000**	**0.001**	**0.006**	1	0.31	0.31	**-0.41**
Total Chl*a*	0.120	0.953	**0.001**	0.080	1	0.078	0.067
BP	0.365	0.673	**0.023**	0.100	0.32	1	-0.23
BR	0.368	0.610	0.078	**0.044**	-0.37	0.282	1

Among picoplankton variables, positive correlations of HB with *Synechococcus* spp. and with picoeukaryotes were recorded. However, no correlation was detected

between *Synechococcus* spp. and picoeukaryotes (Tab.5). Regression analyses revealed stronger relationship of HB with *Synechococcus* spp. ($r^2 = 0.32$, slope = 0.89, df = 31, p = 0.0006) than with picoeukaryotes ($r^2 = 0.17$, slope = 0.39, df = 31, p = 0.016). BP was positively correlated to picoeukaryotes abundance, and BR correlated negatively with TPP.

DISCUSSION

Greater stability in the time dynamics of picoplankton is expected at low latitude oceans (Giovanonni & Vergin, 2002; Heywood et al., 2006). In fact, our results demonstrate that most picoplankton variables (with exception of *Synechococcus*) did not differ between seasons (Tab. 3). Furthermore, environmental seasonality poorly explained temporal variation in abundance and activity of picoplankton at present study. In spite of this, abundance of HB and Peuk, and total chl*a* had a tendency to increase in the period between June and August (Fig. 4*a* and *c,* and Fig. 7), reveling that detection of seasonal cycles in this region perhaps demands data collected over many years (>10 years). Despite failed in detect regular seasonal variations we found considerable month-to-month variation on picoplankton assayed along these 4 years, including inter-annual variation. Total variation in abundance of picoplankton in the current study was higher than expected, reaching ranges equivalent to those found in other microbial observatories located at higher latitudes (Tab.6), where seasonality is well marked and there is a greater variation in SST. This evidence provides a new perspective that microbial dynamics may exhibit less marked seasonal fluctuations compared to mid-high latitude regions, however, if considering the inter-annual changes, the variability in the abundance of picoplankton in this most central portion of the Atlantic can be as expressive as that found towards the poles.

Table 6: Time-series range of picoplankton abundance and timing of maximum abundance in diverse microbial observatories (WCO - Western Channel Observatory; BBMO – Blanes Bay Microbial Observatory; SPOT - San Pedro Ocean Time-Series; BATS - Bermuda Atlantic Time-Series; HOT- Hawaii Ocean Time-Series; SEATS – Southeast Asia Time-Series Station; EAMO – Equatorial Atlantic Microbial Observatory).

Reference	Microbial Observatory	Coordenates	Time-series	HB ($x10^5$ cells ml^{-1})	Syn ($x10^3$ cells ml^{-1})	Peuk ($x10^3$ cells ml^{-1})	Temperature (C°)
Tarran & Bruun (2015)	WCO (Plymouth England)	50° N, 4° W	2007 - 2013	1.5 - 15 summer/ autumn	0.1 – 120 summer	0.2 - 80 summer	8 - 18
Ruiz González *et al.* (2012); Gasol *et al.* (2016)	BBMO (Mediterranean sea)	42° N, 3° E	2008 - 2010	~4 - 12 summer	~1 – 62 Summer	na na	12 - 25
Caron *et al.* (2017)	SPOT (Subtropical North Pacific)	33° N, 118° W	2001 - 2003	3.6 - 41 ns	1.7 – 92 spring/summer	0.05 - 74 spring/ summer	14 - 20
DuRand *et al.* (2001)	BATS (Subtropical North Atlantic)	32° N, 64°W	1989-1994	3.8 - 6.2 spring/ summer	4 – 280 spring	na spring	20 - 29
Campbell *et al.* (1997)	HOT / ALOHA station (Subtropical North Pacific)	23°N, 158°W	1990-1994	2.3 - 7.4 ns	1.1 - 6.3 Winter	0.7 - 6.2 spring	23 - 26
Liu *et al.* (2007)	SEATS (South China Sea)	18° N, 116° E	2001 -2005	6.2 - 12 spring	0.5 – 8 winter /spring	0.5 - 15 winter/ spring	23 - 3
This study	EAMO (Western equatorial Atlantic)	06º S, 35° W	2013-2016	1.4 - 19.5 ns	38.6 – 178 summer	0.36 - 5 ns	24 - 29

na = not available;
ns= not specified

We evidenced that inter-annual variation of total picoplankton was directly related to South oscillation Index or El Niño influence (Fig.6). El Niño may positively affect picoplankton at NE Brazil coast by two main processes: (1) by reducing precipitation as result of tropospheric warming that suppresses atmospheric convection; and (2) by inducing cross-equatorial SST anomalies related to increased upwelling events (e.g. Benguela system in the African east coast) caused by southeasterly wind anomalies near the equator (Xie *et al.*, 2014). Although El Niño influences on Brazilian NE are well recognized, its effects on picoplankton still require more studies since effects on hydrology may vary depending on the intensity of El Niño. Rodrigues *et al.* (2011) discuss that strong and long El Niño events are followed by droughts episodes in the NE Brazil, while in weak and short ones strong positive anomalies in SST at the equatorial western Atlantic occurs.

Heterotrophic bacteria

The dominance of HB cells marked the structure of picoplankton community, with HB corresponding on average to 67% of total picoplankton biomass (Fig. 7) and exceeding *Synechococcus* and picoeukaryotes even during their occasional peaks. Our results are consistent with other studies along Brazilian coast (Andrade *et al.*, 2004; Ribeiro *et al.*, 2017) and in the South Atlantic Ocean, where estimates reveal the percentage of HB varying from 50 to 70% related to prokaryotic picoplankton cells in oligotrophic waters (Landry *et al.*, 1996; Zubkov *et al.*, 1998). HB biomass becomes proportionally more important in ecosystems where photosynthetic biomass is low, with chl *a* concentrations ≤ 0.05-1 µg L^{-1}, as recorded in the present study. Some possible reasons proposed to explain HB dominance in oligotrophic systems are allochthonous C subsidies (e.g. rivers discharges for coastal regions) and decreased bacterivory. Additionally, HB access to nutrients that are not available to phytoplankton (Cotner & Biddanda, 2002) is another possible explanation supported by our results of nutrients concentration, which revealed most part of N available in organic form (easily processed by bacterial extra-cellular enzymes).

Photoautotrophic picoplankton

Synechococcus was the unique picoplankton component that differed between dry and rainy seasons (Tab.3), with peaks occurring in dry season, especially in summer from November to January (Fig. 4*b*). Summer peaks of *Synechococcus* were also recorded in coastal waters of subtropical East China Sea (Jiao *et al.*, 2005), although the same study recorded peaks in winter at open ocean site (Kushiro water). Jiao *et al.* (2005) argued that there is an apparent conflict in seasonal dynamics of *Synechococcus* between coastal and open oceans. They found that water temperature during the winter (6°C) could be a limiting factor near the coast, while at open ocean winter average temperature (20.4°C) was not limiting, but peaks of *Synechococcus* occurred predominantly in mid-latitudes, mostly associated with deepening of mixed-layer depth (Campbell *et al.*, 1997; DuRand *et al.*, 2001; Liu *et al.*, 2007). In this study, temperature was not a limiting factor (maximum variation of 25-29ºC), and nutrients did not showed seasonal variation as well (Fig. S5 and S6). Although, the positive correlation between *Synechococcus* and PAR suggest that increase of *Synechococcus* in the summer is a response to the higher solar radiation.

Picoeukaryotes were two orders of magnitude lower than *Synechococcus* in abundance, similar to what was recorded in southern coast of China (Huang *et al.*, 2009). Picoeukaryotes may be numerically less important than cyanobacteria, however they can be great in terms of C standing stock, showing lower abundances just due to higher grazing pressure (Worden *et al.*, 2004). In agreement, our results revealed low relative biomass of picoeukaryotes, but probably because picoeukaryotes thrive better where the light is scarce and the nutrient concentration is higher, near the bottom of the euphotic zone at tropical open oceans (Vazquez-Dominguez *et al.*, 2008; Partensky *et al.*, 1996). Thus, our surface sampling may have underestimated the contribution of picoeukaryotes to picoplankton in the study area, since it is likely to be more abundant at greater depths.

As picoeukaryotes, *Prochlorococcus* showed very low abundances (< $x10^2$ cells ml^{-1}). In most samples, we did not detect *Prochlorococcus* by flow cytometry analysis. Even though, we have evidences of its existence in our samples by 16S amplicon sequencing (Kavagutti *et al*., in review.). In general, *Prochlorococcus* dominates in most part of the oligotrophic oceans by selective advantages in absorption characteristics and photosynthetic performances (in contrast with *Synechococcus*) (Blanchot & Rodier, 1996, Zubkov *et al.*, 2000; Heywood *et al.*, 2006; Karl & Church, 2014). However, *Synechococcus* can equal or even surpass *Prochlorococcus*, especially in surface waters, since *Prochlorococcus* appears to be quite sensitive to high irradiances (Partensky *et al.*, 1999a; Corsbie & Furnas, 2001; Bergo *et al*., 2017). The light absorption proprieties (e.g. low pigment content and low chl*a* concentration) of *Prochlorococcus* also interfere with ability to detect populations in marine surface samples analyzed by flow cytometry. This problem of detection may depend on the method adopted (Partensky *et al.*, 1999b); and the type of instrument (e.g. BD FACSCanto, BD Accuri C6; Ribeiro *et al*., 2016) and can be the reason of non-detection here.

Bacterial C metabolism

Reduction in variability found in BP and BR in the second half of the study period suggests that interannual variations may also influence microbial metabolism as well as abundance and biomass. For example, 68% of the variance found for BR was relate to the period from February 2013 to September 2014. Although weak correlations have hampered our ability to understand the causes of this process, it is clear that there is a reduction in rates and variability in inter-annual scale. Vaqué *et al.* (2014) found low variability in BP between autumn and spring seasons in 2002-2003, a period under El

Niño influence. While high variance in metabolic rates has been accessed in other studies across Atlantic oceans, but within the range of a year (Vázquez-Domínguez *et al.*, 2008; Hoppe et al., 2002). Despite high variability, our BP estimates were predominantly high, exceeding previous studies in coastal and open oceans. In fact, BP rates can be up to 3 times higher in regions closer to the coast (Biddanda *et al.*, 1994; Vaqué *et al.*, 2014). Higher BP rates associated with coastal waters may be due to the increased energy limitation from inshore to offshore waters (Del Giorgio *et al.*, 2011). Our data was still comparable with southeast coast of Brazil, showing similar BP values (0.2 - 7.29 µg C L^{-1} h^{-1}), even considering that these regions has more eutrophic conditions (Paranhos *et al.*, 2001).

The very high RB variation in the 2013-2014 period, exhibiting even greater fluctuations than BP seems to be controversial. There is a consensus that respiration seems to be much less variable than other processes in water ecosystems (Del Giorgio & Duarte, 2002). The fact that BP can be subsidized by several distinct sources of organic matter reflects its higher potential variability compared with RB, which is largely influenced by temperature. Thus, as temperatures showed low variability across all study period, we decided to disregard data from this high variance period (2013-2014). Considering only data from 2015-2016 the estimated average BR was 5.38 µg C L^{-1} h^{-1}, which is almost half the mean calculated previously. This problem involving BR certainly exerted negative influences on the statistical analysis. Like most of the biotic variables, BR did not present a seasonal signal, despite showing almost regular peaks in March/April period (Fig. 9). Additionally, significant correlations founded for BR with TDS, NO^{2-} and SiO_2, are not very clear and must be further explored. The new average of BR including only data after September 2014, was also closer to that estimated from surface coastal waters by Del Giorgio & Williams (2005) of 3.7 µg C L^{-1} h^{-1}.

The decrease of BR rates and variability in 2015 and 2016, reflected in an increased BGE, from an average of 6% to 25% in the last two years. Nevertheless, low values of BGE (17% on total average) prevailed. In a general way, our measures of BP, BR and BGE agree with previous studies for tropical coastal oceans (Lee *et al.*, 2009) and such studies evidence lower BGE in tropical environments as a result of higher temperatures, higher light exposure and nutrient limitation (Amado *et al.*, 2013). Additional explanation relate to the negative relationship between BGE and C:N ratio, which denotes that low quality substrate (high C:N ratios) reduces bacterial efficiency to produce biomass (Pradeep Ram *et al.*, 2003). Even in a hypereutrophic estuarine

ecosystem of Northeast Brazil (Guenther *et al.*, 2017), where BP, BR and consequently BCD (2.88, 20.64 and 23.52 µg C l^{-1} h^{-1} on average, respectively) were two-fold higher than the rates in the present study (1.56, 10.78 and 11.51 µg C l^{-1} h^{-1}, respectively), low BGE were recorded, with a similar average (13%). This confirms the low efficiency in energy use of bacteria in low latitudes, as reported by Hoppe *et al.* (2002) in a study performed in transects from North to South at Atlantic. We also detected increased BP/BR ratios related to chl*a* concentration (slope = 6.03, R^2=0.41), which suggest an increase in efficiency of substrate utilization by HB during period of higher chl *a* concentrations, and higher photosynthetic biomass. Increased BGE with increasing chl *a* concentrations suggests that phytoplankton substrate release may be the main source of organic matter for bacteria in such cases, even in shallow coastal waters.

High contribution of picoplankton in low-latitude

Predominant high contributions (median equal to 59%) of picoplankton fraction (<3µm) to total chl *a* is an evidence of the tinny cells dominance in pelagic zone of these tropical waters. Such contribution would be even higher if considering *Prochlorococcus* cells, which were not detected by the method adopted here. Our estimates exceeds the 33% contribution of picoplankton observed in a temperate coastal ecosystem located in the southern Bay of Biscay (Calvo-diaz *et al.*, 2008). The lower amplitude of variation in picoplankton contribution (47-73%) than that found by Li *et al.* (1983) in the eastern tropical Pacific Ocean (20-90%) suggest constant high importance of photoautotrophic picoplankton to chl *a* biomass production in the study area. Persistent high picoplankton contribution seems to be unexpected for most coastal waters that are in most cases eutrophic due to riverine inputs and upwelling events (Chavez, *et al.*, 1996). However, since oligotrophic conditions prevail in Equatorial Atlantic Microbial observatory, picoplankton importance was estimated to be high year around.

Maximum contributions occurred during dry seasons (Fig. 5) despite no significant difference (data not shown), coinciding with *Synechococcus* abundance and biomass peaks (Fig. 4*b*). Our results are in agreement with studies performed in temperate coastal environments (e.g. Gasol *et al.*, 2002), which revealed greater contributions of picoplankton (especially of *Synechococcus*) to total chl*a* biomass during summer, when there is greater light intensity and nutritional restriction. Additionally, *Synechococcus* showed a negative correlation with rainfall, reinforcing the idea of photosynthetic prokaryotes dominance during drier periods. On the other hand, the contribution of total

picoplankton decreased during colder (<27ºC) and less saline periods (i.e. July and August), when total chl*a* was maximum (Fig. 8) and micro-nanoplankton (>3µm) equals picoplankton in its contribution to the chl *a* biomass.

Environmental drivers of picoplankton

Coastal environments are influenced by diverse factors such as river and continental discharges, atmospheric changes, winds forces, adjacent water masses, among others, being an ecosystem highly heterogeneous. In the study area, salinity was the key factor with negative influences on abundance of entire picoplankton community and chl *a* (Tab. 4, Fig. S7). This suggest that all mechanisms related with salinity reduction as well riverine inputs, intensive rainfall episodes or less saline outer shelf water masses entrance in the coastal zone might affect picoplankton positively. This influence may arise from the covariation between salinity and nutrients (as previously discussed for nutrients). In fact, we found negative relation between salinity and NH^{4+} (r= -0.37; p=0.05), which is expected since ammonium is often related to a recycled production, more specific of the direct exchange between phytoplankton and HB.

Riverine inputs are able to reduce salinity and bring POC to the coast. However, river discharges are insignificant according to Vital *et al*. (2010) in the study area, since nearby rivers are small and do not contribute to significant amounts of organic matter. We believe that this hypothesis require further investigations, especially taking into account the effects of the tide, because freshwater entrance into the coastal region can be intensified during the ebb tide. Here, even considering the effects tide, we found no difference in nutrients concentrations between samplings made during periods of high or low tides (data not shown).

Rainfall influence was predominantly weak on picoplankton, but it may represent simultaneous impacts with indirect effects. The impacts of rainfall are especially important in upper layers (the top 5m) of the water column (Li *et al*., 1998). For example, rainfall can favor increased POC (r = 0.32; p = 0.006) by organic matter entrance in the coast from rivers and continental sources. In addition, it reduce available radiation through cloud cover (r = -0.58; p < 0.001). In this sense, positive correlations between picoeukaryotes and total chl *a* with POC and TDS reflect that eukaryotic phytoplankton may constitute a significant portion of these organic matter in periods of higher turbulence and suspended particles, during rainy seasons (Tab.2). Water transparency decreased

shortly when higher concentrations of POC and Chl*a* were recorded, preventing solar radiation to reach the ocean floor (Fig. S3). Ruiz-González *et al.*, (2012) and DuRand *et al.*, (2001) argue that POC sets up a good predictor of phytoplankton C and demonstrate that eukaryotic components of phytoplankton seems to be stronger related with POC than prokaryotic ones.

Coastward intrusions bringing cold and nutrient rich waters have never been reported for this region (Castro *et al.*, 2006). However, this may occur if dispersion is efficient enough to transport nutrients in a cross-equatorial gradient. At NE Brazil, strong winds prevail almost the whole year round, mixing nearby water masses (Vital *et al.*, 2010). Wind-induced transport of surface waters, controlled by seasonal displacement of ITCZ (Castellanos *et al.*, 2015) may transport surface water masses westward in a meridional scale across Atlantic and mix adjacent ones (e.g. South Atlantic Central Waters with Tropical or Coastal Waters) in shallower coastal regions. Furthermore, Barth & Hauila (1968) reported topographically-induced small-scale upwelling events that can enhance primary and secondary production at the surface divergent zones between 5°S and 7°S.

All mechanisms abovementioned, are probable weak nutrients sources for picoplankton on this coastal region. The provision of allochthonous nutrients can eventually support what is known as new production of plankton. In fact, nitrate revealed peaks during most rainy season (June and August 2014, 2015 and 2016, Fig. S5), and eventual high concentrations were recorded for other N forms, which would be linked with other processes mentioned above. N concentrations are typically low in oligotrophic oceans (ammonia <0.5 µM; nitrite = 0.1 µM; nitrate = 0.2 µM), while most coastal waters present higher values (ammonia = 25 µM, nitrite = 2 µM; nitrate = 30 µM) according to Sharper (1983). Mean concentrations recorded here (ammonia = 1.72 µM, nitrite = 0.07 µM, nitrate = 1.22 µM) were predominantly close to inferior limits of coastal amplitude. Thus, as nutrient concentration variability was independent from seasonal influences, the mechanisms responsible for these eventual increases of nutrients are still unclear, but can be linked with biological supply and assimilation, in such case by picoplankton.

In spite of eventual nutrients supplies, we are led to believe that secondary bacterial production is predominantly supplied by autotrophic picoplankton exudates. Stronger couplings between bacterial and phytoplankton production (BP:PP) are expected under nutrient limitation conditions (Shiah *et al.*, 2001). The link between heterotrophic bacteria and (pico) phytoplankton occurs through feedback interaction mechanisms based

on the exchange of organic and inorganic compounds (Mague *et al.*, 1980; Karl *et al.*, 1998). This interaction may configure major energy sources for both in certain conditions. This suggest that microbial loop may deeply contribute to energy flow in aquatic food web in these oligotrophic coastal waters. Although we found weak positive relations between components of picoplankton here, we highlight the need of new studies to better describe these relationships in a underexploited area in plankton research. In addition, it is necessary to evaluate the effects of interactions with other components of plankton, such as virioplankton and microzooplankton. The predation by protists (heterotrophic nano flagellates and ciliates) and virus infection can be determinant in reducing the abundance of the entire picoplankton community (Sherr & Sherr, 1994; Brunn *et al.*, 2015). Here, we only evaluate the environmental effects, which in general have been shown to be quite complex.

CONCLUSION REMARKS

We raised three key issues on the dynamic and importance of picoplankton in western equatorial Atlantic coast. At first, we would to investigate if (1) *seasonality explain the dynamics of picoplankton in a scenario of greater environmental stability of tropics.* Our work confirmed the idea that picoplankton in equatorial regions shows great temporal stability in a seasonal scale, but can vary significantly in major time-scales. Clear inter-annual influences on climate caused by El Niño events for example, can be decisive favoring picoplankton even in environments where nano-microplankton would prevail, as in coastal regions.

Second, we would estimate (2) *How important is the picoplankton size fraction to the C budget, considering autotrophic and heterotrophic organisms*. In this sense, we found that autotrophic picoplankton contributes significantly to the total phytoplankton biomass even in a coastal environment. However, it shows lower relative contribution than HB, as described in literature. Increased picoplankton importance (mainly of HB) in warmer conditions has been recently discussed faced with current climate change (Morán *et al*., 2010; Sarmento *et al.*, 2010), and our data provide evidences of these assumptions. Future climate projections for NE Brazil suggest SST increases and rainfall reductions (Marengo *et al.*, 2016). These predictions, jointly with expected increased picoplankton importance in warmer conditions, suggest that gradual shift towards smaller primary producers will have profound implications for marine biogeochemistry and C

sequestration for deep ocean (Litchman *et al.*, 2015). The implications of picoplankton dominance would be great in sense to weaken the flow of energy by adding new trophic levels to aquatic food chain, which reduces the efficiency of energy transfer to higher trophic levels (Sarmento, 2012).

Finally, we wanted to investigate (3) *which environmental factors regulates picoplankton abundance and metabolism (of heterotrophic fraction) in the study area*, and our results revealed that salinity was the main environmental factor with negative effects on most picoplankton variables. Factors driving changes in salinity are still uncertain for the region, but weak environmental relationships found may suggest a greater importance of biological interactions for picoplankton dynamic. Thus, we highlight the need of more studies in this central portion of the planet, given the increasing importance of these microbes for maintenance of global climate and the marine trophic chain in a scenario of global warming.

REFERENCES

Agawin NSR, Agustí S (2005) *Prochlorococcus* and *Synechococcus* cells in the central Atlantic Ocean: distribution, growth and mortality (grazing) rates. Vie Milieu, v.55, n. 3/4, p. 165-175

Amado MA, Meirelles-Pereira F, Vidal LO, Sarmento H, Suhett AL, Farjalla VF, Cotner JB, Roland F (2013) Tropical freshwater ecosystems have lower bacterial growth efficiency than temperate ones. *Frontiers in microbiology* **4**:1-8

Andrade, A.M. Gonzalez, J.L. Valentin & R. Paranhos (2004) Bacterial abundance and production in the southwest Atlantic Ocean. *Hydrobiologia **511**:* 103–111

Arrigo KR (2005) Marine microorganisms and global nutrient cycles. *Nature* **437**: 349 - 355

Azam, F, Fenchel T, Field JG, Gray JS , Meyerreil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* **10**: 257–263.

Azam F, Worden AZ (2004). Microbes, molecules, and marine ecosystems. *Science* **303**: 1622-1624

Barth R., Hauila G (1968) Estudos volumétricos em plâncton capturado na costa brasileira entre Recife e Cabo Orange. *Publ. Inst. Pesq. Mar* **28:** 1-14

Berggren M, Lapierre JF, del Giorgio PA (2011) Magnitude and regulation of bacterioplankton respiratory quotient across freshwater environmental gradients. *The ISME Journal 1–10*

Bergo NM, Signori CN, Amado AM, Brandini FP, Pellizari VH (2017). The Partitioning of Carbon Biomass among the Pico- and Nano-plankton Community in the South Brazilian Bight during a Strong Summer Intrusion of South Atlantic Central Water. *Fron. Mar. Sci.* **4**

Biddanda B, Opsahl S, Benner R (1994) Plankton respiration and carbon flux through bacterioplankton on the Louisiana shelf. *Limnol. Oceanogr*. **39** (6): 1259-1275

Bidigare RR, Ondrusek ME (1996) Spatial and temporal variability of phytoplankton pigment distributions in the central equatorial Pacific Ocean. *Deep-sea Res II* **43**: 809-833.

Blanchot J, Rodier M (1996) Picophytoplankton abundance and biomass in the western tropical Pacific Ocean during the 1992 El Niño year: results from flow cytometry. *Deep-Sea Res. I* **43**:877-895

Briand E, Pringault O, Jacquet S, Torreton JP (2004) The use of oxygen microprobes to measure bacterial respiration for determining bacterioplankton growth efficiency. *Limnol. Oceanogr*.406–416

Brum JR, Ignacio-Espinoza JC, Roux S, Doulcier G, Acinas SG, et al. (2015) Patterns and ecological drivers of ocean viral communities. *Science* **348**: 6237

Calvo-Díaz A, Morán XAG, Suárez LA (2008) Seasonality of picophytoplankton chlorophyll a and biomass in the central Cantabrian Sea, southern Bay of Biscay. *Journal of Marine Systems* **72**:271–281

Campbell L, Liu H, Nolla HA, Vaulot D (1997) Annual variability of phytoplankton and bacteria in the subtropical North Pacific Ocean at station ALOHA during the 1991–1994 ENSO event. *Deep-Sea Res. I* **44**:167–192

Caron DA, Connell PE, Schaffner RA, Schnetzer A, Fuhrman JA, Countway PD, Kim DY (2017) Planktonic food web structure at a coastal time-series site: I. Partitioning of microbial abundances and carbon biomass. *Deep–Sea Research Part I* **121**: 14–29

Castellanos P, Pelegrí JL, Campos EJD, Rosell-Fieschi M, Gasser M (2015) Response of the surface tropical Atlantic Ocean to wind forcing. *Progress in Oceanography* **134:** 271–292

Castro BM, Frederico Brandini P, Pires-Vanin AMS, Miranda LB (2006) Multidisciplinary oceanographic processes on the western Atlantic continental shelf between 4°N and 34°S In: The Sea, Vol. 14 - The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses, Chapter 8

Chavez FP, Buck KR, Service SK, Newton J, Barber RT (1996) Phytoplankton variability in the central and eastern tropical Pacific. *Deep-Sea Res. II*, **43**:835-870

Cotner JB, Biddanda BA (2002) Small Players, Large Role: Microbial Influence on Biogeochemical Processes in Pelagic Aquatic Ecosystems. *Ecosystems* **5**: 105–121

Crosbie ND, Furnas MJ (2001) Abundance, distribution and flow-cytometric characterization of picophytoprokaryote populations in central (17°S) and southern (20°S) shelf waters of the Great Barrier Reef. J. Plankton Res. *23*: 809–828.

Dandonneau Y, Deschamps PY, Nicolas JM, Loisel H, Blanchot J, Montel Y, Thieuleux F, Bécu G (2004) Seasonal and interannual variability of ocean color and composition of phytoplankton communities in the North Atlantic, equatorial Pacific and South Pacific. *Deep-Sea Res. II* **51**: 303–318

Del Giorgio PA, Bird DF, Prairie YT, Planas D (1996) Flow cytometric determination of bacterial abundance in lake plankton with the green nucleic acid stain SYTO 13. *Limnol. Oceanogr.* **41**: 783–789

Del Giorgio PA, Duarte CM (2002) Respiration in the open ocean. *Nature* **420**:379-384

Del Giorgio P. A. and Williams P. J. (2005) Respiration in Aquatic Ecosystems. *Journal of Plankton Research*, **8**:113–114

Del Giorgio PA, Condon R, Bouvier T, Longnecker K, Bouvier C, Sherr,E, Gasol JM (2011) Coherent patterns in bacterial growth, growth efficiency, and leucine metabolism along a northeastern Pacific inshore–offshore transect. *Limnol. Oceanogr.* **56**(1): 1–16

DuRand MD, Olson RJ, Chisholm SW (2001) Phytoplankton population dynamics at the Bermuda Atlantic time series station in the Sargasso Sea. *Deep-Sea Res. II* **48**: 1983–2003

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical Controls and Feedbacks on Ocean Primary Production. *Science* **281**: 200 - 206

Fenchel T (1988) Marine plankton food chain. *Ann. Rev. Ecol. Syst*. **19**:19 - 38

Flombaum P, Gallegos JL, Gordillo FA et al. (2013) Present and future global distributions of the marine Cyanobacteria Prochlorococcus and Synechococcus. *Proc. Natl Acad. Sci* **110**: 9824–9829

Furhman JA, Sleeter TD, Carlson CA, Proctor LM (1989) Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. *Mar. Ecol. Prog. Ser*. **57**: 207-217

Gasol JM, del Giorgio PA (2000) Using flow cytometry for counting natural planktonic bacteria and understanding the structure of planktonic bacterial communities. *Sci Mar.* **64**: 197-224

Gasol JM, Duarte CM (2000) Comparative analyses in aquatic microbial ecology: how far do they go? *FEMS Microbiol. Ecol.* **31**: 99 - 106

Gasol JM, Pedrós-Alió C, Vaqué D (2002) Regulation of bacterial assemblages in oligotrophic plankton systems: results from experimental and empirical approaches. *Antonie van Leeuwenhoek* **81***:* 435–452

Gasol JM, Cardelús C, Morán XAG, Balagué V, Forn I, Marrasé C, Massana R, Pedrós-Alió C, Sala MM, Simó R, Vaqué D, Estrada M (2016) Seasonal patterns in phytoplankton photosynthetic parameters and primary production at a coastal NW Mediterranean site. *Sci. Mar.* **80S1**: 63-77

Giovannoni JS, Vergin KL (2012) Seasonality in Ocean Microbial Communities. *Science* **335**: 671-676

Grasshoff K, Erhardt M & Kremling K (1999) Methods of Seawater Analysis.Verlag-Chemie, Weinhein, 159-187

Guenther M, Gonzalez-Rodriguez E, Flores-Montes M, Araújo M, Neumann-Leitão S (2017) High bacterial carbon demand and low growth efficiency at a tropical hypereutrophic estuary: importance of dissolved organic matter remineralization. *Brazilian Journal of Oceanography* **65**(3):382-391

Herbland A, Le Bouteiller A, Raimbault P (1985) Size structure of phytoplankton biomass in the equatorial Atlantic Ocean. *Deep-Sea Res* **32** (7): 819-836

Heywood JL, Zubkov MV, Tarran GA, Fuchs BM, Holligan PM (2006) Prokaryoplankton standing stocks in oligotrophic gyre and equatorial provinces of the Atlantic Ocean: Evaluation of inter-annual variability. *Deep-Sea Res II* **53**: 1530–1547

Hoppe HG, Gocke K, Koppe R, Begler C (2002) Bacterial growth and primary production along a north–south transect of the Atlantic Ocean. *Nature* **416**: 168-171

Huang B, Schopf PS, Shukla J (2004) Intrinsic Ocean–Atmosphere Variability of the Tropical Atlantic Ocean. *America. J. Climate* **17**: 2058

Huang B, Lin X, Hong H (2009) Spatial and temporal variations of Synechococcus and picoeukaryotes in the Taiwan Strait, China. *Chinese Journal of Oceanology and Limnology* **27**:22-30

Instituto Nacional de Meteorologia - http://www.inmet.gov.br/portal/

Jiao N, Yang Y, Hong N, Ma Y, Harada S, Koshikawa H, Watanabe M (2005) Dynamics of autotrophic picoplankton andheterotrophic bacteria in the East China Sea. *Continental Shelf Research* **25** 1265–1279

Karl DM, Hebel DV, Bjorkman K, Letelier RM (1998) The role of dissolved organic matter release in the productivity of the oligotrophic North Pacific Ocean. *Limnol Oceanogr* **43**: 1270–1286

Karl DM, Church MJ (2014) Microbial oceanography and the Hawaii Ocean Time-series programme. *Nature* **12**: 1-15

Kavagutti VS, Rigonato J, Menezes M, Ferrera I, Logares R, Amado AM, Paranhos R, Gasol JM, Sarmento H (in review) Drivers of coastal microbial communities in contrasting latitudes. In prepation for re-submission.

Kirchman DL (1992) Incorporation of thymidine and leucine in the subarctic Pacific: Application to estimating bacterial production. *Mar. Ecol. Prog. Ser*. **82**: 301–309

Kirchman DL (2008) Microbial Ecology of the Oceans (second edition). Wiley, New York, pp. 261–288.

Landry MR, Kirshtein J, Constantinou J (1996) Abundances and distributions of picoplankton populations in the central equatorial Pacific from 12”N to 12”S,14O”W. *Deep-Sea Res II* **43:** 871-890

Lee CW, Bong CW, Hii YS (2009) Temporal Variation of Bacterial Respiration and Growth Efficiency in Tropical Coastal Waters *Applied and Environmental Microbiology*, **75** (24): 7594–7601

Legendre L, Rassoulzadegan F (1995) Plankton and nutrient dynamics in marine waters. *Ophelia* **41**: 153-172

Lewis WMJ (1976) Surface/volume ratio: implications for phytoplankton morphology. *Science* **192**: 885–887

Li WKW, Rao DVS, Harrison WG, Smith JC, Cullen JJ, Irwin B, Platt T (1983) Autotrophic picoplankton in the tropical ocean. *Science* **219**: 292-295

Li X, Xui CH, Adamec D, Lau KM (1998) Impacts of precipitation in the upper ocean in the western Pacific warm poll during TOGA-COARE. *Journal of Geophysical Research* **103**: 5347-5359

Liu H, Chang J, Tseng CM, Wen LS, Liu KK (2007) Seasonal variability of picoplankton in the Northern South China Sea at the SEATS station. *Deep-Sea Res.* II **54**: 1602–1616

Litchman E, Pinto PT, Edwards KF, Klausmeier CA, Kremer CT, Thomas MK (2015) Global biogeochemical impacts of phytoplankton: a trait-based perspective. *Journal of Ecology* **103:** *1384*–1396

Liu H, Chang J, Tseng CM, Wen LS, Liu KK (2007) Seasonal variability of picoplankton in the Northern South China Sea at the SEATS station. *Deep-Sea Res II* **54**: 1602–1616

Longhurst, AR, Pauly D (1987) Ecology of tropical oceans. Academic Press, San Diego

Luhtala H, Tolvanen H (2013) Optimizing the Use of Secchi Depth as a Proxy for Euphotic Depth in Coastal Waters: An Empirical Study from the Baltic Sea. *SPRS Int. J. Geo-Inf.* **2**: 1153-1168

Mague TH, Friberg E, Hughes DJ, Morris I (1980) Extracellular release of carbon by marine-phytoplankton – a physiological approach. *Limnol Oceanogr* **25**: 262–279

Marañón E, Holligan PM, Varela M, Mouriño B, Bale AJ (2000) Basin-scale variability of phytoplankton biomass, production and growth in the Atlantic Ocean. *Deep-Sea Res I* **47**:825–857

Marañón E, Behrenfeld MJ, González N, Mouriño B, Zubkov MV (2003) High variability of primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from phytoplankton biomass and size structure. *Mar Ecol Prog Ser* **257** : 1-11

Marengo JA, Torres RR, Alves LM (2016) Drought in Northeast Brazil—past, present, and future. *Theor Appl Climatol* **124**: 3-4

Marie D, Partensky F, Vaulot D (1996) Application of the novel DNA dyes YOYO-1, YOPRO-1 and Picogreen for flow cytometric analysis of marine prokaryotes. *Appl. Environ. Microbiol*. **62**: 1649-1655

Marie D, Partensky F, Jacquet S, Vaulot D (1997) Enumeration and cell cycle analysis of natural populations of marine picoplankton by flow cytometry using the nucleic acid stain SYBR Green I. *Appl. Environ. Microbiol*. **63**: 186-193

Marie D, Shi XL, Rigaut-Jalabert F, Vaulot D (2010) Use of flow cytometric sorting to better assess the diversity of small photosynthetic eukaryotes in the English Channel. *FEMS Microbiol Ecol* **72**:165–178

Martiny, A.C., Vrugt, J.A., Primeau, F.W., and Lomas, M.W. (2013). Regional variation in the particulate organic carbon to nitrogen ratio in the surface ocean. *Global Biogeochemical Cycles* **27**: 723-731

Massana R (2011) Eukaryotic Picoplankton in Surface Oceans. *Annu Rev Microbiol* **65**:91-110

Morán XAG, Lopez-Urrutia A, Calvo-Diaz A, Li WKW (2010) Increasing importance of small phytoplankton in a warmer ocean. *Global Change Biology* **16:** 1137–1144

Moreno-Ostos E, Fernández A, Huete-Ortega M, Mouriño-Carballido B, Calvo-Díaz A, Morán XAG, Marañón E (2011) Size-fractionated phytoplankton biomass and production in the tropical Atlantic. *Sci Mar* **75**: 379-389

Moreno-Ostos E (2012) Expedición de circunnavegación Malaspina 2010: Cambio global e exploración de la biodiversidad del oceáno global. Libro Blanco de Métodos y Técnicas de Trabajo Oceanográfico. Consejo Superior de Investigaciones Científicas. Madrid, 2012

Moore LR, Goericke R, Chisholm SW (1995) Comparative physiology of *Synechococcus* and *Prochlorococcus*:influence of light and temperature on growth, pigments, fluorescence and absorptive properties. *Mar. Ecol. Prog. Ser.* **116**: 259 - 275

Moser GAO, Castro NO, Takanohashi RA et al. (2016) The influence of surface low-salinity waters and cold subsurface water masses on picoplankton and ultraplankton distribution in the continental shelf off Rio de Janeiro, SE Brazil. *Continental Shelf Research* **120**: 82–95

Nimer E (1989) Climatologia do Brasil. 20. ed. Rio de Janeiro: IBGE

Norland S, Heldal M, Tumyr O (1987) On the Relation between Dry Matter and Volume of Bacteria *Microb. Ecol.* **13** (2): 95-101

Not F, del Campo J, Balagué V, de Vargas C, Massana R (2009) New Insights into the Diversity of Marine Picoeukaryotes. *PLoS ONE* **4**:7143

Paranhos R, Andrade L, Mendonça-Hagler LC, Pfeiffer WC (2001) Coupling bacterial abundance with production in a polluted tropical coastal bay. Pp. 117-132. In: Faria BM Farjalla VF and Esteves FA (eds.) Aquatic Microbial ecology in Brazil. Series Oecologia Brasiliensis, vol IX PPGE-UFRJ, Rio de Janeiro, Brazil

Parsons TR, Maita Y, Lalli CM (1984) A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, Oxford, 173

Partensky F, Blanchot J, Lantoine F, Neveuxs J, Dominique M (1996) Vertical structure of picophytoplankton at different trophic sites of the tropical northeastern Atlantic Ocean. *Deep-Sea Res I* **43** (8): 1191-1213

Partensky F, Blanchot J, Vaulot D (1999a) Differential distribution and ecology of *Prochlorococcus* and *Synechococcus* in oceanic waters: a review. *Bulletin de l'Institut Océanographique* **19**:457–476

Partensky F, Hess WR, Vaulot D (1999b) *Prochlorococcus*, a marine photosynthetic prokaryote of global significance. *Microbiology and Molecular Biology Reviews* **63**:106–127

Pérez V, Fernández E, Marañón E, Serret P, Varela R, Bode A, Varela M, Varela MM, Morán XAG, Woodward EMS, Kitidis V, García-Soto C (2005) Latitudinal distribution of microbial plankton abundance, production, and respiration in the Equatorial Atlantic in autumn 2000. *Deep-Sea Res I* **52**: 861–880

Pomeroy LR (1974) The Ocean's Food Web, A Changing Paradigm. *BioScience* **24** (9): 499–504

Pradeep-Ram AS, Nair S, Chandramohan D (2003) Bacterial growth efficiency in the tropical estuarine and coastal waters of Goa, southwest coast of India. *Microb. Ecol.* **45**:88–96

Redfield AC, Ketchum BH, Richards FA *(*1963) The influence of organisms on the composition of sea water, p. 26–77. In Hill MN (ed.) *The sea, vol. 2.* Wiley-Interscience, New York, NY

Ribeiro CG, Dominique M, Santos AL, Brandini FP, Vaulot D (2016) Estimating microbial populations by flow cytometry: Comparison between instruments. *Limnol. Oceanogr.: Methods* **14**: 750–758

Ribeiro CG, Santos AL, Dominique M, Pellizari VH, Brandini FP, Vaulot D (2016) Pico and nanoplankton abundance and carbon stocks along the Brazilian Bight. *PeerJ* 4:e2587

Rodrigues RR, Haarsma RJ, Campos EJD, Ambrizzi T (2011) The Impacts of Inter–El Niño Variability on the Tropical Atlantic and Northeast Brazil Climate. *Journal of Climate* **24**: 3402 – 3422

Ruiz-Gonzaález C, Lefort T, Galí M, Sala MM, Sommaruga R, Simo R, Gasol JG (2012) Seasonal patterns in the sunlight sensitivity of bacterioplankton from Mediterranean surface coastal waters. *FEMS Microbiol Ecol* **79:** 661–674

Sarmento H (2010) New paradigms in tropical limnology: the importance of the microbial food web. *Hydrobiologia* **686**:1–14

Sarmento H (2012) New paradigms in tropical limnology: the importance of the microbial food web. *Hydrobiologia* **686**:1–14

Schattenhofer M, Fuchs BM, Amann R, Zubkov MV, Tarran GA, Pernthaler J (2009) Latitudinal distribution of prokaryotic picoplankton populations in the Atlantic Ocean. *Environ. Microbiol.* **11**(8): 2078–2093

Sharp JH (1983) The distribution of inorganic nitrogen and dissolved and particulate organic nitrogen in the sea. In: Nitrogen in the marine environment (Ed. By E.G. Carpenter & D.G. Capone) pp. 1-35. Academic press, New York.

Sherr EB, Sherr BF (1988) Role of microbes in pelagic food webs: a revised concept. *Limnol Oceanogr* **33**:1225-1227

Shiah FK, Chen TW, Gong GC, Chen CC, Chiang KP, Hung JJ (2001) Differential coupling of bacterial and primary production in mesotrophic and oligotrophic systems of the East China Sea. *Aquat. Microb. Ecol.* **23**: 273–282

Sieburth JM, Smetacek, V, Lenz J (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnol. Oceanogr*. **23** (6) : 1256–1263.

Silva M, Moacyr Araujo M, Servain J, Penven P, Lentini CAD (2009) High-resolution regional ocean dynamics simulation in the southwestern tropical Atlantic. *Ocean Modelling* **30**: 256–269

Smith DC, Azam F (1992) A simple, economical method for measuring bacterial protein syntesis rates in seawater using ^{3}H-leucine. *Mar. Microbial. Food Webs* **6**: 107–114.

Sterner RW, Clasen J, Lampert W,Weisse T (1998) Carbon: phosphorus stoichiometry and food chain production. *Ecol. Lett.* **1**: 146 - 150

Tarran GA, Brunn JT (2015) Nanoplankton and picoplankton in the Western English Channel: abundance and seasonality from 2007–2013. *Progress in Oceanography* **137**: 446-455

Taylor AG, Landry MR, Freibott A, Selph KE, Gutiérrez-Rodríguez A (2016) Patterns Of Microbial Community Biomass, Composition And HPLC Diagnostic Pigments In The Costa Rica Upwelling Dome. *J. Plankton Res*. **38**(2): 183–198

Vaulot D, Eikrem W, Viprey M, Moreau H (2008) The diversity of small eukaryotic phytoplankton (≤3 μm) in marine ecosystems *FEMS Microbiol Rev **32**:* 795–820

Vaqué D, Alonso-Sáez L, Arístegui J, Agustí S, Duarte CM, Sala MM, Vázquez-Domínguez E, Gasol JM (2014) Bacterial production and losses to predators along an open ocean productivity gradient in the Subtropical North East Atlantic Ocean. *J. Plankton Res* **36**(1): 198–213

Vázquez-Domínguez, E, Duarte C, Agustí S, Jürgens K Vaqué D, Gasol J (2008) Microbial plankton abundance and heterotrophic activity across the Central Atlantic Ocean. *Progress in Oceanography* **79**: 83-94

Vital H, Gomes MP, Tabosa WF, Frazão EP, Santos CLA and Júnior JS *(*2010) Characterization of the brazilian continental shelf adjacent to Rio Grande do Norte State, NE Brazil. *Brazilian Journal of Oceanography*, **58**:43-54

Viviani DA, Björkman KM, Karl DM, Church MJ (2011) Plankton metabolism in surface waters of the tropical and subtropical Pacific Ocean. *Aquat Microb Ecol* **62**: 1-12

Xie SP, Carton JA (2004) Tropical Atlantic Variability: Patterns, Mechanisms, and Impacts. In: Wang C (ed) Earth Climate: The Ocean-Atmosphere Interaction, Geophysical Monograph, AGU, Washington

Waterbury JB, Watson SW, Guillard RRL, Brand LE (1979) Widespread occurrence of a unicellular, marine, planktonic, cyanobacterium. *Nature* **277**: 293–29

Welschmeyer NA (1998) Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnol. Oceanogr.* **39**(8) 1985 - 1992

White PA, Kalff J, Rasmussen JB, Gasol JM (1991) The effect of temperature and algal biomass on bactenal production and specific growth rate in freshwater and marine habitats. *Microb. Ecol.* **21**: 99-118

Worden AZ, Nolan JK, Palenik B (2004) Assessing the dynamics and ecology of marine picophytoplankton: the importance of the eukaryotic component. *Limnol. Oceanogr.* **49**: 168–179

Zubkov MV, Sleigh MA, Tarran GA, Burkill PH, Leakey RJG (1998) Picoplankton community structure on an Atlantic transect from 50° N to 50° S. *Deep-Sea Res. I* **45**: 1339–1355

Zubkov MV, Sleigh MA, Burkill PH, Leakey RJG (2000) Picoplankton community structure on the Atlantic Meridional Transect: a comparison between seasons. *Progress in Oceanography* **45**:369–386

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Chapter 6 : Violation of Independence – Part I. In: Mixed effects models and extensions in ecology with R. Springer, New York, NY

SUPPLEMENTARY MATERIAL

Table S1: Conversion coefficients for calculation of euphotic zone from data of secchi disk depth in coastal waters proposed in Luhtala & Tolvanen (2013).

Category	Secchi	Coeficient (m)
Q1	< 2.1	3.32
Q2	2.1-3.6	3.08
Q3	3.6-4.5	2.69
Q4	>4.5	2.35

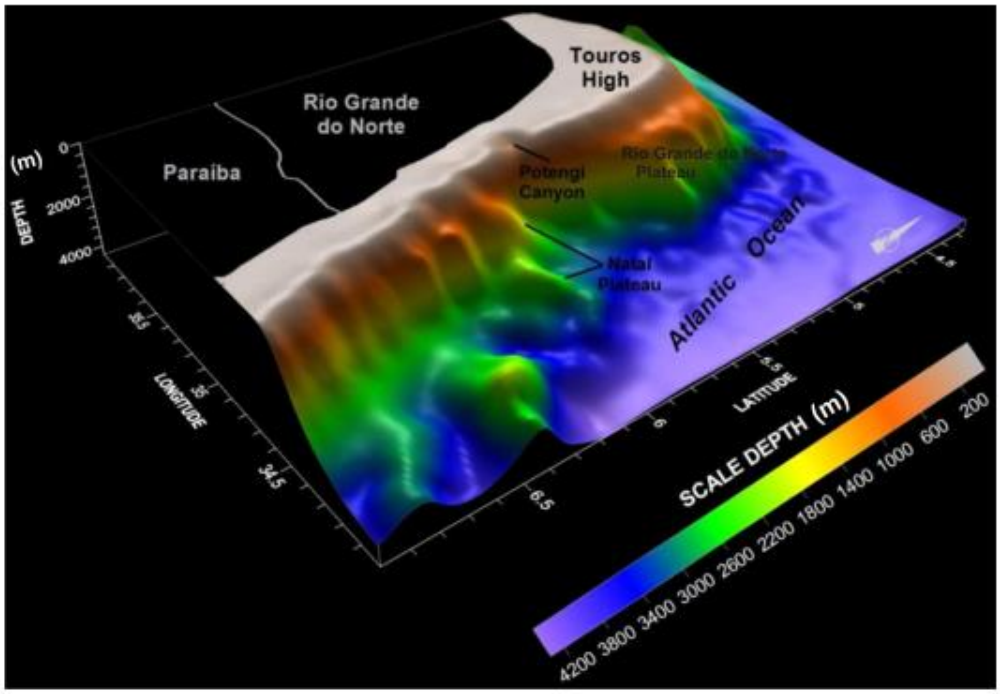

Figure S1: Digital model of Rio Grande do Norte shelf. Source: Vital et al., 2010.

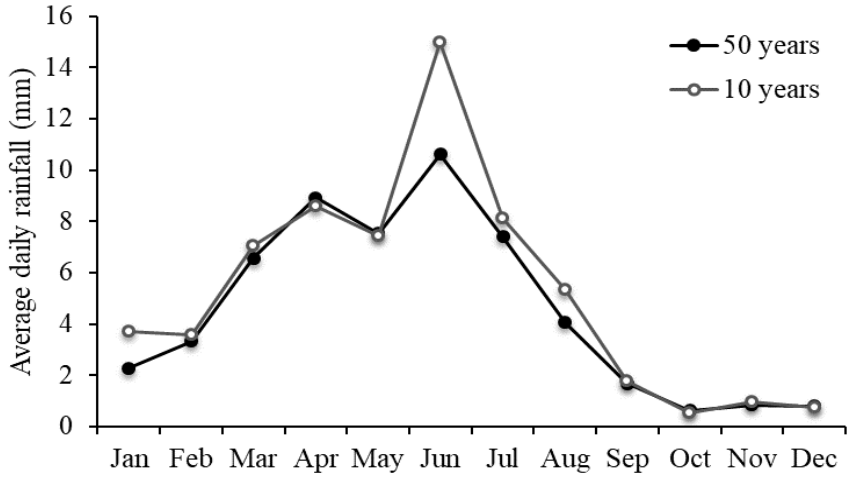

Figure S2: Plot of **d**aily rainfall averages by month for the last 50 years and 10 years in east coast of Rio Grande do Norte state, used to determine rainy (March-July) and dry (August-February) seasons in this study, in accordance with Nimer (1989).

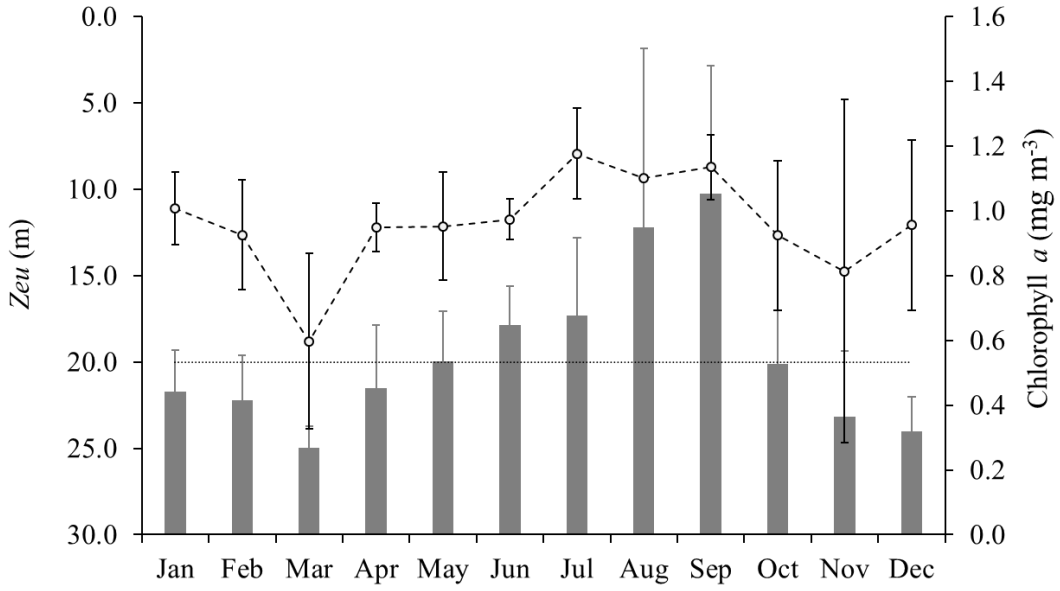

Figure S3: Vertical profile of mean euphotic zone depth (*Zeu*- dashed line) by month and chl*a* concentration (bars) variation along 2013-2016 study period in western equatorial Atlantic coast. Error bars denotes standard deviation.

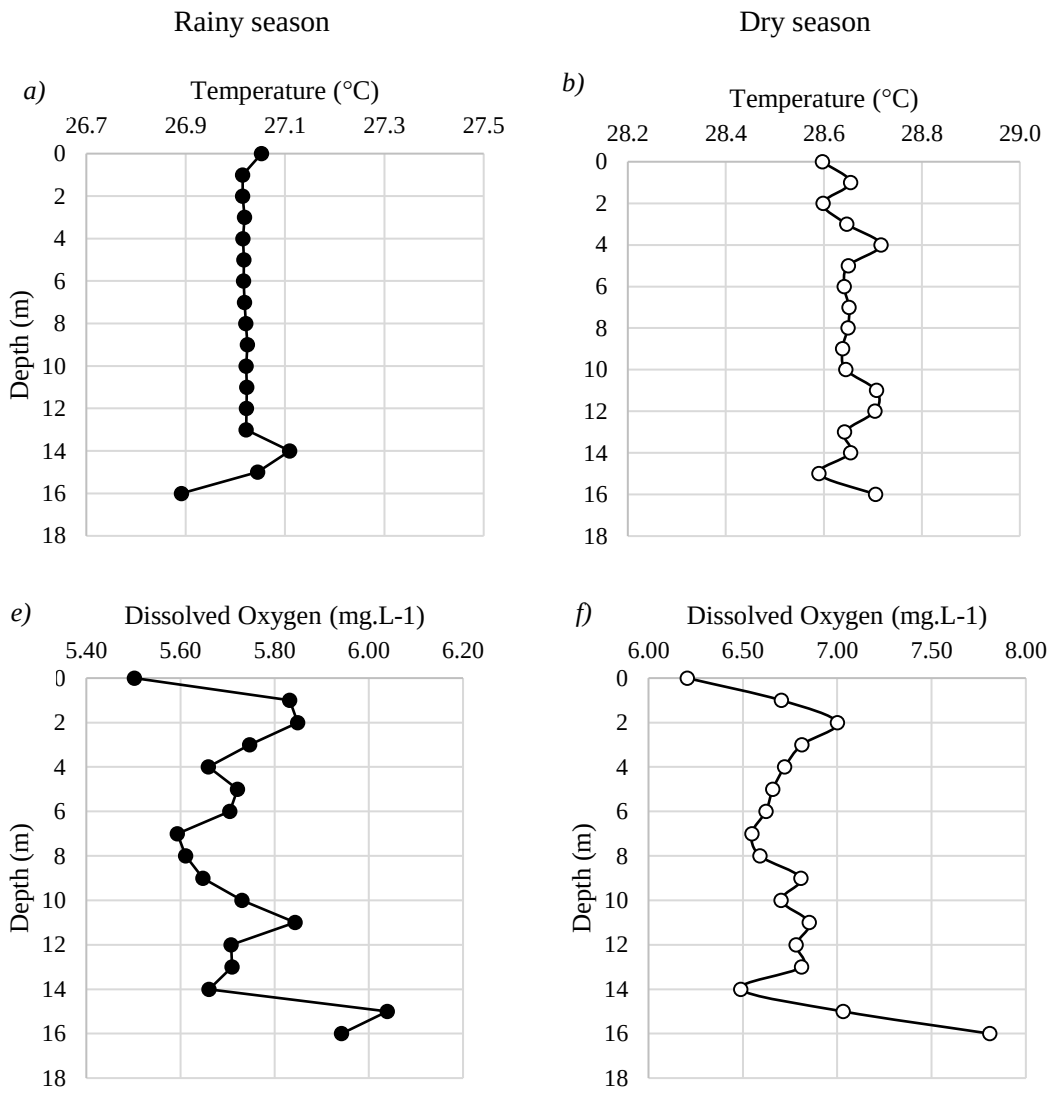

Figure S4: Vertical profiles of Temperature and Dissolved Oxygen mean values in rainy season on the left and dry season on the right.

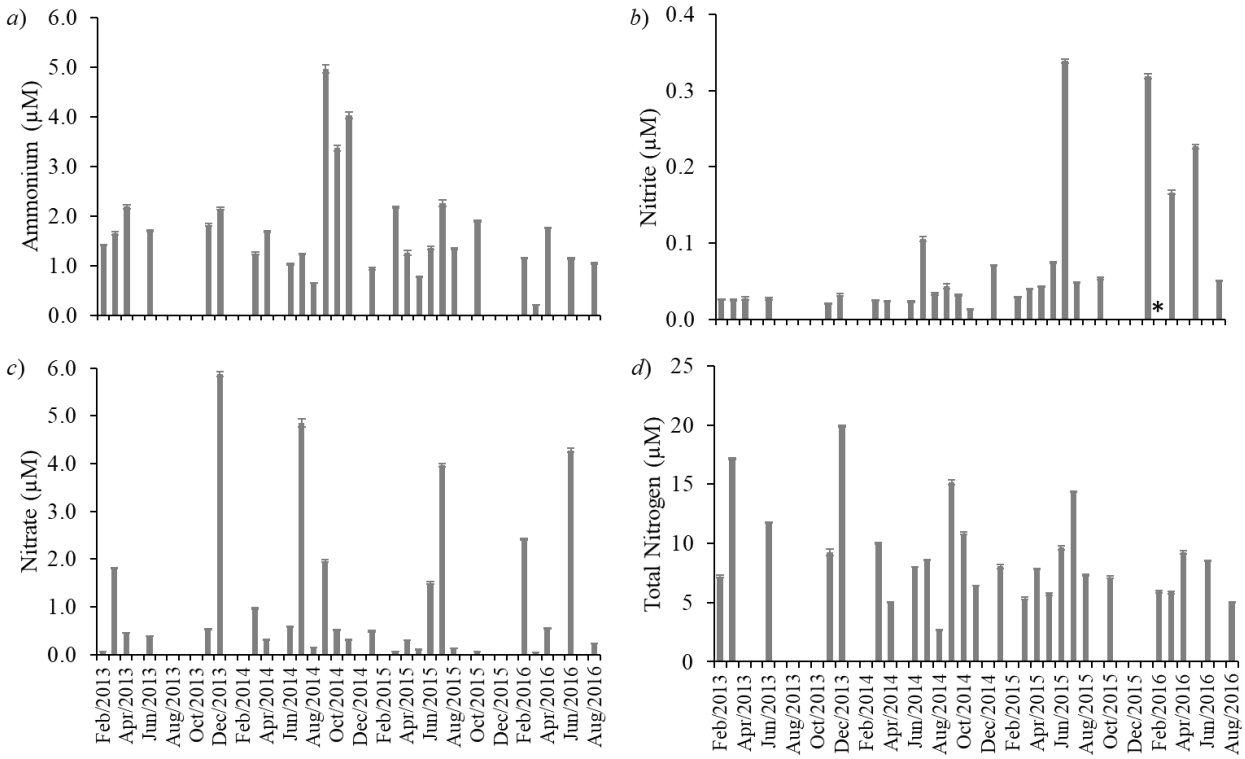

Figure S5: Variation of a) ammonium, b) nitrite, c) nitrate and d) total nitrogen along 2013-2016 at study site. The missing values are samples that were lost during thawing or months when there was no field sampling. The * stands for data below the detection limit

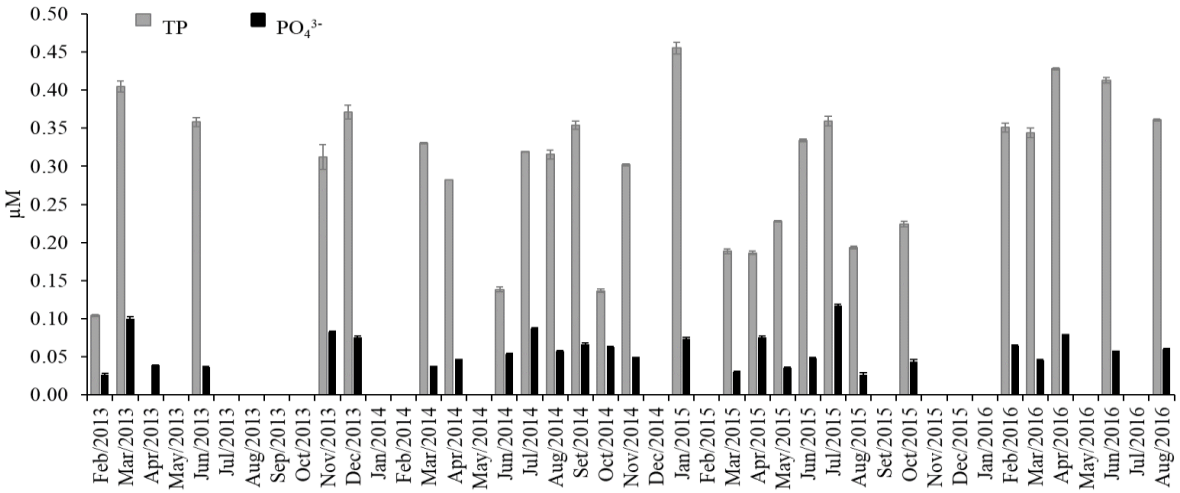

Figure S6: Variation of Phosphorus concentration along the study period (2013-2016) in western equatorial Atlantic coast of Brazil.

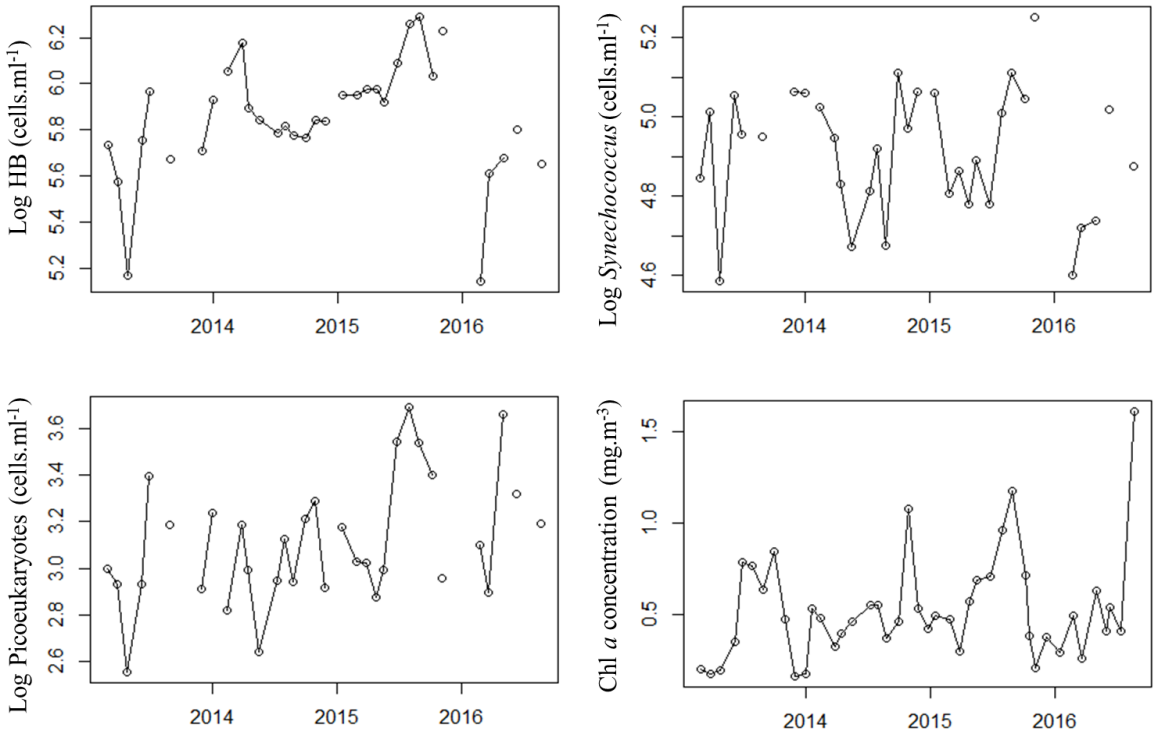

Figure S7: Time series distribution of picoplankton components: a) Heterotrophic Bacteria, b) Synechococcus and c) Picoeukaryotes and d) Chlorophyll *a* concentration during 2013-2016 in Equatorial Brazilian coast.

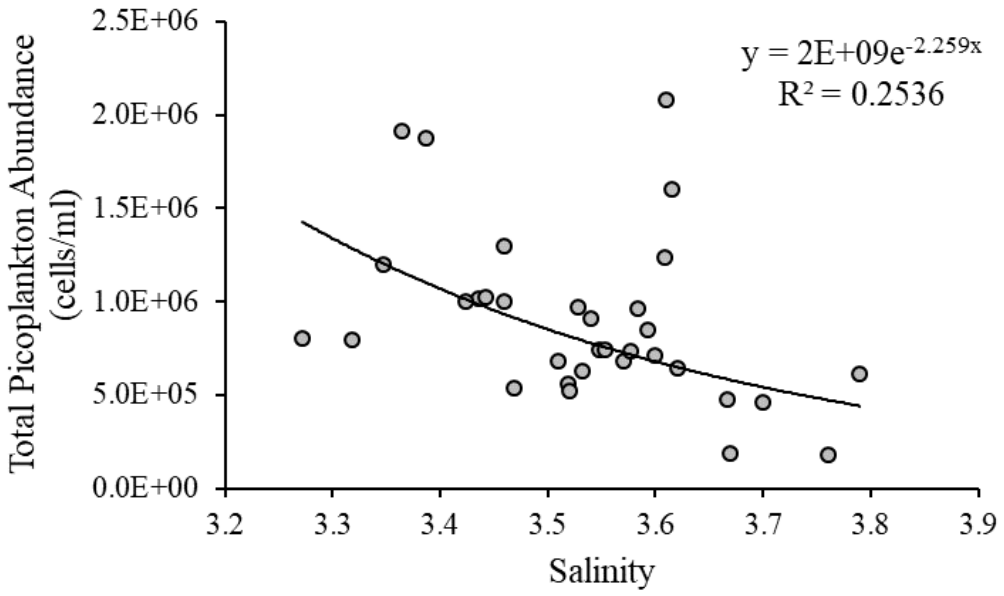

Figure S8: Plot of total picoplankton abundance and Salinity relation.

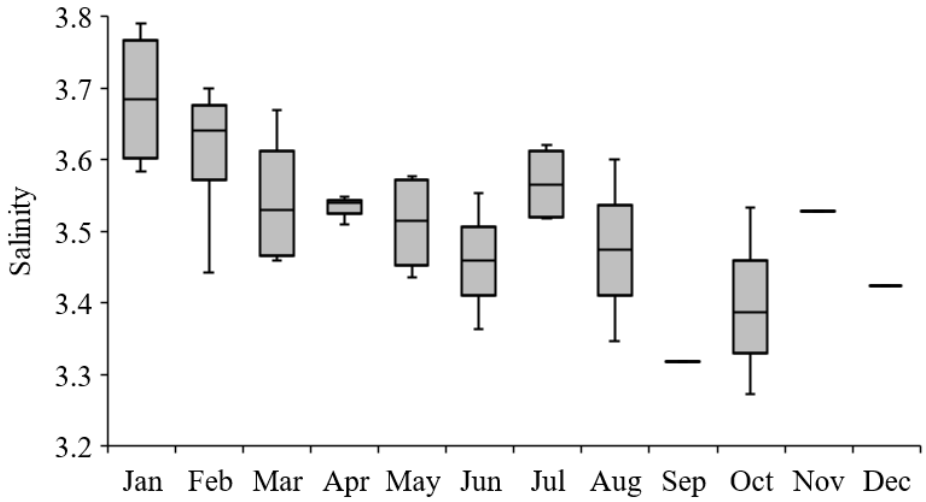

Figure S9: Annual variation in salinity (median, box are 3º e 5º quartiles, whiskers are minimum and maximum).